THE UNIVERSITY OF ALBERTA

AN ECOLOGICAL STUDY OF THE PRIMARY PRODUCER LEVEL OF THE SUBALPINE SPRUCE-FIR ECOSYSTEM OF BANFF AND JASPER NATIONAL PARKS, ALBERTA

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled, "AN ECOLOGICAL STUDY OF THE PRIMARY PRODUCER LEVEL OF THE SUBALPINE SPRUCE-FIR ECOSYSTEM OF BANFF AND JASPER NATIONAL PARKS, ALBERTA", submitted by Charles Edward Beil in partial fulfilment of the requirements for the degree of Master of Science.

ABSTRACT

The objectives of this study were: (1) to characterize the primary producer level of the subalpine spruce-fir ecosystem of Banff and Jasper National Parks by description of its structural and phytosociological attributes and (2) to relate these attributes to the environment.

Utilizing aerial photographs and field observations, 13 stands were located in Banff and five in Jasper. Quantitative data were obtained for structural attributes of four strata and their component species. Measured environmental factors included: physical and chemical properties of the soil, slope angle, aspect, elevation and stand history.

The vascular flora consisted of 113 species--six trees, 15 shrubs, and 92 herbs and dwarf shrubs. Most species showed both geographic and altitudinal range restrictions.

The sampled spruce-fir ecosystem was structurally simple, consisting of only four recognizable strata. The bryophyte-lichen stratum was the best-developed, covering 57% of the ground; the tree stratum had a mean cover of 50%; the herb-dwarf shrub stratum had a mean cover of 26% and the shrub stratum was the most poorly-developed with a mean cover of 16%.

The sampled spruce-fir ecosystem was floristically simple in that 25 species were largely responsible for the development of the four strata. The most important species were: trees, _Picea engelmannii_ and _Abies lasiocarpa_, both of which showed distinct life-history patterns; shrubs, _Menziesia glabella_;

herbs and dwarf shrubs, *Vaccinium scoparium*, *Vaccinium membranaceum*, *Lycopodium annotinum* and *Arnica cordifolia*; bryophytes, *Hylocomium splendens*, *Pleurozium schreberi*.

The relation between vegetation structure and environment was analysed using simple correlation and multiple regression. Regression equations utilizing sampled edaphic, physiographic and historic variables accounted for much of the variation in the structure of the tree stratum. Regression equations for the lower strata included attributes of the tree stratum as well as physical variables. Structure of the lower strata appeared to be controlled by development of the tree stratum.

The relation between sizes of species populations and the environment was analysed using multiple regression. Spruce and fir had very different environmental dependencies, suggesting that they show habitat preferences. Regression equations showed that species of lower strata were less dependent on the development of the tree stratum than was the vegetation structure.

A two-dimensional ordination of stands in which the spatial separation of stands was inversely proportional to their degree of similarity was constructed. Most species and influential environmental factors showed distinct patterns and optimal centres when plotted on the ordination.

It was concluded that the spruce-fir ecosystem of Banff and Jasper is a continuously varying vegetation within its range of occurrence and is closely related to other mountain and boreal ecosystems.

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I INTRODUCTION

A Consideration of the Subalpine Forest in the Rocky Mountains

The subalpine zone, bordering on the alpine tundra, is the uppermost forested zone of the Rocky Mountains. This zone occupies an altitudinal range of approximately 2,000 feet and is characteristically dominated throughout its extent by a climatic climax of Engelmann spruce (*Picea engelmannii* Parry) and subalpine fir (*Abies lasiocarpa* Nutt.) (Daubenmire 1943).

In his description of the Life Zones of North America, Merriam (1898) considered the subalpine forest along with other mountain forests as part of the transcontinental coniferous forest which he termed the "Boreal Region." This region included all the continent from the Polar seas southward to the 49th parallel and southward extensions along the principal mountain ranges (Daubenmire 1938). According to Oosting and Reed (1952), Merriam placed the subalpine spruce-fir forest into both the Hudsonian zone (northern forested part of Canada and mountain forests just below timberline) and the Canadian zone (southern forested part of Canada and a belt below the Hudsonian zone in the mountains).

A survey of the literature pertaining to the

subalpine forest of the Rocky Mountains can logically be divided into the four botanical provinces used by Daubenmire (1943) in his description of vegetation zonation in the Rocky Mountains. He designated these provinces as Far-Northern, Northern, Central and Southern and assigned them the following geographical limits. The division between the Far-Northern and Northern provinces occurs at about the latitude of central Alberta and British Columbia; a line running east and west through the centre of the state of Wyoming separates the Northern and Central provinces; the line separating the Central and Southern provinces occurs just a little south of and parallel to the northern borders of the states of New Mexico and Arizona.

Far-Northern Rocky Mountains

The Far-Northern Rocky Mountains contain a subalpine forest in which Engelmann spruce, subalpine fir, white spruce [*Picea glauca* (Moench) Voss] and black spruce [*Picea mariana* (Miller) B.S.P.] are the characteristic trees (Daubenmire 1943, 1953). Halliday and Brown (1943) reported the same list of dominants with the addition of western white spruce [*Picea glauca* var. *albertiana* (S. Brown) Sarg.]. They further stated that Engelmann spruce reaches its northern limit in the Far-Northern province at approximately the 57th parallel.

Northern Rocky Mountains

The Northern Rocky Mountain division, especially the portion located in northern Montana and Idaho, has been much more extensively described. Rydberg (1900) divided Montana into three phytogeographic regions one of which he called the subalpine region. He described this region as a mesophytic forest formation consisting of Engelmann spruce, lodgepole pine (*Pinus contorta* Loudon var. *latifolia* Engelm.), limber pine (*Pinus flexilis* James), whitebark pine (*Pinus albicaulis* Engelm.), lowland white fir (*Abies grandis* Lindl.) and Douglas fir [*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco]. In a later publication Rydberg (1915) stated more specifically that the subalpine forest contained Engelmann spruce, subalpine fir lodgepole pine, limber pine, Douglas fir, whitebark pine, alpine larch (*Larix lyallii* Parl.), aspen (*Populus tremuloides* Michx.) and Mountain hemlock [*Tsuga mertensiana* (Bong.) Sarg.]. He further stated that alpine larch and subalpine fir are restricted to the subalpine zone and that aspen occurs largely as a successional tree on recently burned areas.

More recent published reports of the subalpine forests of the Northern Rockies list fewer tree species as being characteristic of the zone. Larsen (1930) gave an account of subalpine forests on both the east and west

sides of the Continental Divide. For forests on the west slope of the Bitterroot Mountains he listed mountain hemlock as the climax species with Engelmann spruce and subalpine fir inhabiting northern exposures and moist situations and lodgepole pine, Douglas fir and whitebark pine occurring on exposed drier sites. Larsen indicated that the subalpine forests of the east slope of the Rockies in central Montana are dominated by Engelmann spruce and subalpine fir with whitebark pine as a constant associate, and that Douglas fir and lodgepole pine occur only in the lower reaches of the subalpine zone.

Daubenmire (1952) gave Engelmann spruce and subalpine fir as the characteristic dominants of forests in northern Idaho and stated that neither is entirely restricted to the subalpine, although both are uncommon in the next lower zone. In the same report he listed whitebark pine, alpine larch and mountain hemlock as being restricted to and playing climax roles on certain habitats in the subalpine zone.

Patten (1963), working in the Madison Range of Montana, rated the subalpine forest as a climax association dominated by Engelmann spruce and subalpine fir, with fir becoming the more important dominant near timberline. He included lodgepole pine, limber pine, whitebark pine and Douglas fir as subordinate tree species of the forest

and noted that the ground cover is either absent due to a thick litter layer or is composed of mosses and a few herbs.

The portion of the subalpine forest lying in Alberta has been incompletely described, and most of the published reports available deal with the forest from a plant successional point of view. De Grace (1950) listed only four tree species as predominating in the subalpine forest of Alberta. He stated that Engelmann spruce and subalpine fir dominate at high elevations, that western white spruce occurs in southern Alberta and that lodgepole pine occurs throughout the area as a major part of young stands but a very minor part of old stands.

Bloomberg (1950), in his consideration of successional aspects of the spruce-fir forest near Blairmore, Alberta, reported that lodgepole pine regenerated thickly on burns, stagnated at about 150 years and was gradually succeeded by spruce and fir to form a climax forest of great age and stability. The paradoxical part of his report was his observation that the climatic types are apparently unable to perpetuate themselves; "spruce regeneration was conspicuous by its scarcity and fir, ... was hardly profuse enough to fill in sparse spots and gaps." Bloomberg concluded that the age-class distribution of these stands was directly attributable to fire and that without regularly occurring fires of a catastrophic nature

the climax type becomes decadent. Cormack (1953), working on the east slope of the Alberta Rockies, listed white, black and Engelmann spruce, subalpine fir, lodgepole pine and aspen as the natural cover of the slopes with Douglas fir occurring in the south and limber pine occurring locally on exposed ridges. He recognized two trends of succession leading to the stable spruce-fir climax: (1) spruce and pine to climax and (2) pine to climax. In the first, spruce and occasionally fir become established at the same time as pine; in the second, the early stages of succession are characterized by either open or dense stands of pine and spruce enters later. Cormack emphasized the stability of the spruce-fir climax and gave a very different report than that of Bloomberg on regeneration. He stated: "Reproduction and subsequent growth of spruce and fir occurs under openings in the forest canopy due to windthrow of overmature trees. Here, large numbers of spruce and fir seedlings may be found on almost every moss-covered windthrow." Horton (1956) listed Engelmann spruce and subalpine fir as tolerant dominants of the subalpine forest and rated lodgepole pine as an important successional tree, particularly in stands having a fire origin.

Central Rocky Mountains

Accounts of the subalpine forests in this region go back to 1878 when Rothrock published a paper dealing

with the vegetation of certain portions of Colorado and listed a few trees of the higher altitudes: lodgepole pine, blue spruce (Picea pungens Engelm.), ponderosa pine (Pinus ponderosa Doug.), subalpine fir, limber pine and bristlecone pine (Pinus aristata Engelm.) (Oosting and Reed 1952).

Ramaley (1907) and Robbins (1910) stated that Engelmann spruce is the characteristic tree of the subalpine forest of Colorado and that subalpine fir and limber pine are secondary species. Young (1907), in making a thorough description of the forest formations of Boulder County, Colorado, named the Pinus flexilis formation, the Pinus contorta formation, the Pseudotsuga menziesii-Picea engelmannii formation, the Picea engelmannii-Abies lasiocarpa formation and the aspen society as component parts of the subalpine zone.

In a description of the vegetation of Long's Peak, Colorado, Cooper (1908) said that the upper forested zone was composed of the Pinus flexilis society, which has reached the climatic limit on the high ridges, and the Picea engelmannii society, which is still advancing on north slopes and in canyons of the region.

Cary (1911) described the Canadian zone in northern Colorado as consisting of extensive forests of aspen and lodgepole pine along with the lower part of the Engelmann spruce belt. He noted that the Canadian zone in

southern Colorado is composed of the same species plus white fir (Abies concolor Lindl.). In the same paper Cary stated that in the Hudsonian zone of Colorado there occurs a forest belt of varying width dominated by Engelmann spruce and subalpine fir with bristlecone pine being present at timberline.

Engelmann spruce and aspen were listed by Rydberg (1915) as characteristic species of the Colorado subalpine zone, together with subalpine fir, bristlecone pine and occasionally limber pine as secondary species. He also stated that Engelmann spruce is often found in the next lower zone and that bristlecone pine occurs only on southern slopes.

Cary (1917) wrote that the Canadian zone of Wyoming is very uniform in composition, dominated by Engelmann spruce and subalpine fir with a scattering of lodgepole pine, aspen, Douglas fir, and blue spruce. He also observed that throughout Wyoming the forest of the Hudsonian zone is composed of essentially Engelmann spruce and subalpine fir except in the northwest portion where whitebark pine is also present. However, in Jackson Hole Wildlife Park, Wyoming, which is within this northwest region, Reed (1952) stated that only Engelmann spruce and subalpine fir are present. He further stated that both species show good evidence of self-perpetuation in the area.

Whitfield (1933), in his survey of the vegetation of the Pike's Peak region of Colorado, said the subalpine forest is dominated by Engelmann spruce with bristlecone pine and limber pine becoming important associates near timberline. He made no mention of the occurrence of subalpine fir in the area.

Clements (1928) listed the subalpine forest as one of the climax forests of North America and called it the Picea-Abies formation.

Sperry (1936) and Cain (1943) stated that the subalpine forest of northern Colorado is usually exclusively composed of Engelmann spruce and subalpine fir although on lower, drier sites some lodgepole pine and Douglas fir occur.

Some indication as to successional patterns in the subalpine forest of the Central Rocky Mountains was given by Ives (1941). He stated that if the climax forest of spruce and fir is removed, it will be succeeded by limber pine on windswept exposed ridges and by lodgepole pine in more sheltered areas. He further observed that aspen may form a subclimax forest in the lower reaches of the subalpine. Stahelin (1943) gave a much more detailed account of secondary succession in the subalpine following fire. He stated that the subclimax prevailing in secondary succession has a strong influence on the rate of recovery

of the climax spruce-fir forest and so divided the subalpine forest zone into three broad types: (a) burns within the altitudinal distribution of lodgepole pine, (b) burns outside the distribution of pine but within the altitudinal distribution of aspen and (c) burns outside the altitudinal distribution of both pine and aspen. In types (a) and (b) a subclimax of pine or aspen is quickly formed providing favourable environments for the establishment of spruce and fir but in type (c) a thick turf subclimax of sedges and grasses forms, evidently preventing the establishment of spruce and fir for many years or even centuries.

Fitcher (1939), Blake (1945) and Oosting and Reed (1952) all worked in the isolated Medicine Bow Mountains of Wyoming and all reported that the subalpine forest is almost exclusively dominated by Engelmann spruce and subalpine fir with lodgepole pine present as a minor constituent.

West of the Continental Divide, where elevation permits, the subalpine forest of the Central Rockies occurs throughout western Wyoming, western Colorado and Utah (Oosting and Reed 1952).

Dixon (1935) described the subalpine forest of south-central Utah and stated that Engelmann spruce is the most abundant tree and in some situations the only one, but usually it is accompanied by subalpine fir. She

further stated that aspen and Douglas fir enter the spruce-fir complex in the lower reaches of the subalpine forest. Ellison (1954) assigned the same general species composition to the subalpine forest of the Wasatch Plateau in western Utah. He noted that limber pine occurs on south, steep, rocky slopes and that spruce and fir are usually confined to northern exposures. He also indicated that in primary succession on talus slopes Engelmann spruce and subalpine fir invade as pioneer species.

Langenheim (1962), in her description of the vegetation of the Crested Butte area, Gunnison County, Colorado, said the subalpine forest is dominated by Engelmann spruce and subalpine fir and characterized by unevenness of age and sizes of trees, together with numerous standing dead individuals. She also noted that the composition of the undergrowth is relatively uniform although there is some influx of alpine herb species near timberline.

Southern Rocky Mountains

In the Southern Rockies, subalpine fir (Abies lasiocarpa) is replaced by its variety corkbark fir [Abies lasiocarpa var. arizonica (Merr.) Lemm.] which together with Engelmann spruce dominate the subalpine forest (Daubenmire 1943).

Merriam (1890), in his study of the San Francisco Mountains region of Arizona, made what was probably the

first description of vegetation zonation in the Southern Rocky Mountains. He stated that Engelmann spruce and bristlecone pine are the characteristic trees of the Hudsonian zone (9,200-10,500 ft) and that these same species in a dwarfed condition form the timberline. Corkbark fir is found associated with Engelmann spruce at elevations below 9,200 ft.

Baily (1913), working in New Mexico, noted that the subalpine forest forms a very narrow band and is dominated by Engelmann spruce and corkbark fir, bristlecone pine and white fir.

A description of the subalpine forest in Arizona was made by Pearson (1920). He wrote that Engelmann spruce is the dominant tree and corkbark fir, bristlecone pine and aspen are common associates. He further stated that limber pine occurs in the lower part of the subalpine but is really a characteristic tree of the next lower vegetation zone.

Merkle (1954), in a description of the spruce-fir community of the Kaibab Plateau, Arizona, listed a total of 45 vascular species of which seven were trees. He stated that Engelmann spruce, subalpine fir, white fir and aspen are the most important trees on ridge tops and northern exposures; Douglas fir and ponderosa pine occur on south slopes and blue spruce occurs only at the lower edges of the subalpine community.

Autecology of Engelmann Spruce and Subalpine Fir

Synecological studies should be "supplemented by at least a synopsis of whatever is known concerning the relationship of the dominants of communities, in the cardinal phases of their life histories, to the environment which surrounds them." (Oosting and Reed 1952).

Habitat Conditions

Soils in the Rocky Mountains are generally young and well-defined profiles are a rarity. However, some of the deepest soils in the Central Rockies are found under forests dominated for the most part by Engelmann spruce. Spruce makes its best growth on moderately deep, well-drained silt and clay loam soils or on alluvial soils where an accessible water table is more important than the physical properties of the soil. It does not make good growth on shallow, dry, coarse-textured soils. Subalpine fir, on the other hand, can tolerate these poorer soil conditions and thus soils too wet or too dry for spruce will often support fir (U.S.D.A. Forest Service 1965).

Sexual Reproduction

Sexual reproduction of both species follows a similar pattern. The staminate cones ripen and pollen is wind-disseminated in the late spring or early summer. The cones mature in mid-September to early October and the

seeds ripen in late September to mid-October. Wind dispersal of seed begins in September and is usually completed by the end of October. However, in the case of spruce some seed continues to fall well into winter (U.S.D.A. Forest Service 1965).

Engelmann spruce begins bearing cones between the ages of 16 and 25 years. Maximum seed production is attained by dominant trees at the age of 200 to 250 years. Lowdermilk (1925), working in Montana, rated spruce as a heavy seed producer with good seed crops at intervals of every three or four years. He also stated that some individual trees are good producers even in the off years.

Subalpine fir begins bearing cones at an age of about 20 years. It reaches maximum seed production when about 150 to 200 years of age. Subalpine fir is rated as a good seed producer, better even than Engelmann spruce (Le Barron and Jemison 1953). Good seed crops are borne on an average of every three years with light crops in the intervening years. However, total failures occur occasionally (U.S.D.A Forest Service 1965).

Seedling Establishment, Development and Survival

Hodson and Foster (1910) observed that fir is much less exacting as to seedbed than is spruce but they considered moisture to be the all-important environmental

factor in the seedbed for both species. The importance of soil moisture to the establishment of spruce and fir seedlings has been emphasized by many authors, notably Lowdermilk (1925) who contended that conservation of surface soil moisture during the critical dry period is essential for spruce seedling establishment, and Day (1964) who stated that soil moisture is the most important environmental factor controlling the establishment and regeneration of both Engelmann spruce and subalpine fir.

A second requirement for the establishment of seedlings is a low light intensity. Korstian (1925), while experimenting with nursery stock, observed that three-fourths shade favours both the germination and survival of spruce seedlings. Day (1964) substantiated this observation for spruce and expanded it to include fir, when he observed that most spruce and fir seedlings become established in heavily-shaded microenvironments.

Engelmann spruce is apparently intolerant of high temperatures and cannot adjust to them even when moisture is available (Pearson 1920; Roeser 1924). Day (1964) suggested that spruce is sensitive to aspect, being found mostly on cool north and northwest slopes, whereas, fir seedlings occur equally well on these cool aspects and on warmer intermediate ones.

Opinion is virtually unanimous that Engelmann

spruce seedling establishment is best on exposed mineral soil or decaying wood and very poor on thick forest duff (litter and partially decayed organic matter on the forest floor) (Hodson and Foster 1910; Lowdermilk 1925; Fisher 1935; McCullough 1948; Cormack 1953; Smith 1955; Horton 1959). It is also agreed that while fir can establish on bare soil or decaying wood, it finds forest duff an equally suitable seedbed because of its initial rapid root growth which allows it to penetrate quickly the organic layer and reach moister lower levels of the soil. Presumably it is this lack of seedbed preference which accounts for the greater numerical superiority of fir reproduction over spruce in natural restocking of forests (Lowdermilk 1925; Oosting and Reed 1952; Horton 1956). However, according to Oosting and Reed (1952), even though a high number of fir seedlings become established, their survival rate is low, whereas the reverse is true of spruce. Thus Engelmann spruce maintains a position of relative dominance in the association.

Asexual Reproduction

Both Engelmann spruce and subalpine fir are able to reproduce vegetatively by layering particularly near their upper altitudinal limits (Cooper 1911; Cain 1941). It has been observed that spruce very seldom layers under closed forest conditions, whereas, the major part of fir

reproduction in some instances may be due to layering (Horton 1959; Langenheim 1962).

Growth to Maturity

The root systems of both spruce and fir are shallowly located but spread out widely from the stem, thus anchoring the trees well, so that areas of widespread windthrow are uncommon in subalpine forests (Oosting and Reed 1952).

Of the two trees, spruce attains the greatest height and size. Mature Engelmann spruce is often 80 to 100 ft tall (U.S.D.A. Forest Service 1965) with stem diameters of up to 40 inches (Oosting and Reed 1952). Mature fir, on the other hand, reaches 60 to 100 ft in height and attains stem diameters of 18 to 24 inches. According to Oosting and Reed (1952), spruce is a much longer-lived tree than fir, with an average life-span of about 500 years, whereas, fir upon reaching an age of 300 years is considered to be overmature. Hansen (1940) found that the growth rates of the two trees differ; spruce shows a greater radial increment in its younger stages while fir shows greater growth as it becomes older.

Both spruce and fir have the ability to withstand long periods of suppression (Oosting and Reed 1952; Horton 1956, 1959). An extreme example of the ability of spruce

to withstand suppression was found by Oosting and Reed when they observed an individual four inches in diameter with 400 annual rings. Fir when released from suppression will make good diameter growth. The response to release appears to be more closely associated with numbers of remaining competitors than age at release or degree of suppression (Stetter 1958). Spruce when released from suppression also grows rapidly and soon outgrows its common associates, like subalpine fir (Garman 1957).

Principal Physical and Biotic Enemies

(The following summary is taken from U.S.D.A. Forest Service 1965).

Both spruce and fir will succumb easily to fire because of their relatively thin bark layers and because of the persistence of highly-inflammable dead lower limbs.

Both trees are plagued by a host of biotic enemies in the form of insects and fungi. The spruce budworm (*Choristoneura fumiferana* Clem.) can cause severe defoliation of spruce and especially of fir. The only other potentially dangerous insect enemy of spruce is the spruce bark beetle (*Dendroctonus engelmannii* Hopk.) to which old-growth spruce is very susceptible. The black-headed budworm (*Acleris variana* Fern.) and the western balsam bark beetle (*Dryocoetes confusus* Sw.) are two additional insect enemies of subalpine fir and may at times be very

destructive.

The most common diseases of Engelmann spruce are caused by the wood-rotting fungi: *Fomes pini* (Thore ex Fr.) Karst., *Polyporus tomentosus* Fr., *Peniophora luna* Rom. and *Stereum sanguinolentum* (Alb. and Schw. ex Fr.) Fr. Two brown rots, *Fomes pinicola* (Schwartz ex Fr.) Cke. and *Coniophora puteana* (Schum. ex Fr.) Karst. and the spruce broom rust, *Peridermium coloradense* (Diet.) Arth. and Kern, have recently been suggested as possible causes of wind-throw amongst spruce trees.

The fungi most commonly causing devastation of fir trees are the balsam fir rust fungus (*Melampsorella caryopayllacearum* Schroet.) and various wood-rotting fungi. Some of the more common wood-rotters are: brown stringy rot [*Echinodotium tinctorium* (Ell. and Ev.) Ell. and Ev.], red heart rot (*Stereum sanguinolentum*), red ring rot (*Fomes pini*), brown cubical rot (*Coniophora puteana*) and white pocket rot [*Polyporus abietinus* (Dicks.) Fr.]. These rots may not themselves destroy the trees but will certainly make them more susceptible to wind breakage.

Small rodents may have harmful effects on regeneration of spruce and fir trees by eating available seed. Large herbivores are reported by Oosting and Reed (1952) to cause severe damage to conifers only if they are present in epidemic numbers. The same authors do, however,

mention that the yellow-haired porcupine (Erethizon dorsatum ssp. epixanthum Brandt) causes destruction of both spruce and fir by blazing or girdling the trees.

Races and Hybrids

There are no recognized races or varieties of Engelmann spruce (U.S.D.A. Forest Service 1965). However, natural hybridization between Engelmann spruce and other members of the genus *Picea* does occur where ranges overlap. In the Central Rocky Mountains, natural crosses between Engelmann and Colorado blue spruce have been observed (U.S.D.A. Forest Service 1965). In the Northern and Far-Northern Rocky Mountains, Engelmann spruce interbreeds freely with white spruce (Halliday and Brown 1943; Moss 1955; Wright 1955; Garman 1957; Horton 1959). Horton considered much of the spruce in subalpine regions of Alberta to be a result of this hybridization and has observed differences in the flowers, shoots, needles, and cones of the two species and their hybrids. Wright (1955), in his study of the genus *Picea*, proved by morphological and genetical evidence a close affinity between Engelmann and white spruce and concluded that western white spruce is actually the product of their hybridization.

In the case of subalpine fir, there are no reported hybrids and only one recognized variety, corkbark fir, which occurs in the Southern Rocky Mountains (Daubenmire 1943; U.S.D.A Forest Service 1965).

II STATEMENT OF OBJECTIVES

This study in the subalpine zone of Banff and Jasper National Parks was undertaken with two main objectives in mind. (1) A synthesis of the general character of the primary producer level of the spruce-fir forest ecosystem by description of its structural and phytosociological attributes. (2) An examination of selected physical and botanical environmental components of the area and their relation to the vegetation and flora.

It is beyond the scope of this study to provide detailed information on the climate, geology, soils and past history of the subalpine region. Much of this information, although by no means a complete record, has been previously obtained by Federal Government agencies and independent investigators.

There is at the present time no complete record of the spruce-fir climax throughout its subalpine range in the Rocky Mountains. It is hoped that the results of this comparative study will add to an understanding of the known variations and relationships of the flora, vegetation and habitats in this widespread subalpine ecosystem.

III METHODS USED FOR SELECTION AND LOCATION OF STANDS

Criteria for Selection of Stands

To ensure uniform sampling areas, a set of vegetational, environmental and historical criteria were drawn up.

Vegetational Criteria

(1) Seventy-five per cent of the basal area of the living trees occupying the overstory of the stand had to be composed of Engelmann spruce and subalpine fir.

(2) The stand had to be in a state of maturity, having individuals of spruce reaching a dbh (stem diameter at breast height) of 12 inches and individuals of fir reaching a dbh of 9 inches.

(3) The stand had to show evidence of self-perpetuation (i.e., seedlings, transgressives and saplings had to be present as well as mature trees).

(4) To guard against selection of successional, even-aged forests, overmatured dead individuals of spruce and fir either standing or fallen had to be present.

(5) The overstory vegetation of the stand had to be of a uniform nature (i.e., having no noticeable changes in structure or composition).

Environmental Criteria

(1) The slope angle of the stand had to be greater than 3°.

(2) The aspect (slope exposure) had to be constant for the stand to avoid differing environmental conditions that correspond to changing exposures.

(3) The stand had to be located within the first 2,000 ft of elevation below the tree limit [lower boundary of the Krummholz zone (Hustich 1952)].

(4) A uniform soil layer had to be present throughout the extent of the stand. This was tested by probing the ground with a steel rod to detect the presence of underlying rock strata.

(5) No noticeable environmental gradients (excluding elevation and its dependent correlates) could be present in the stand.

Historical Criteria

(1) The stand could not show any sign of human interferance such as logging.

(2) Evidence of recent natural catastrophes such as fire or wind could not be present in the stand.

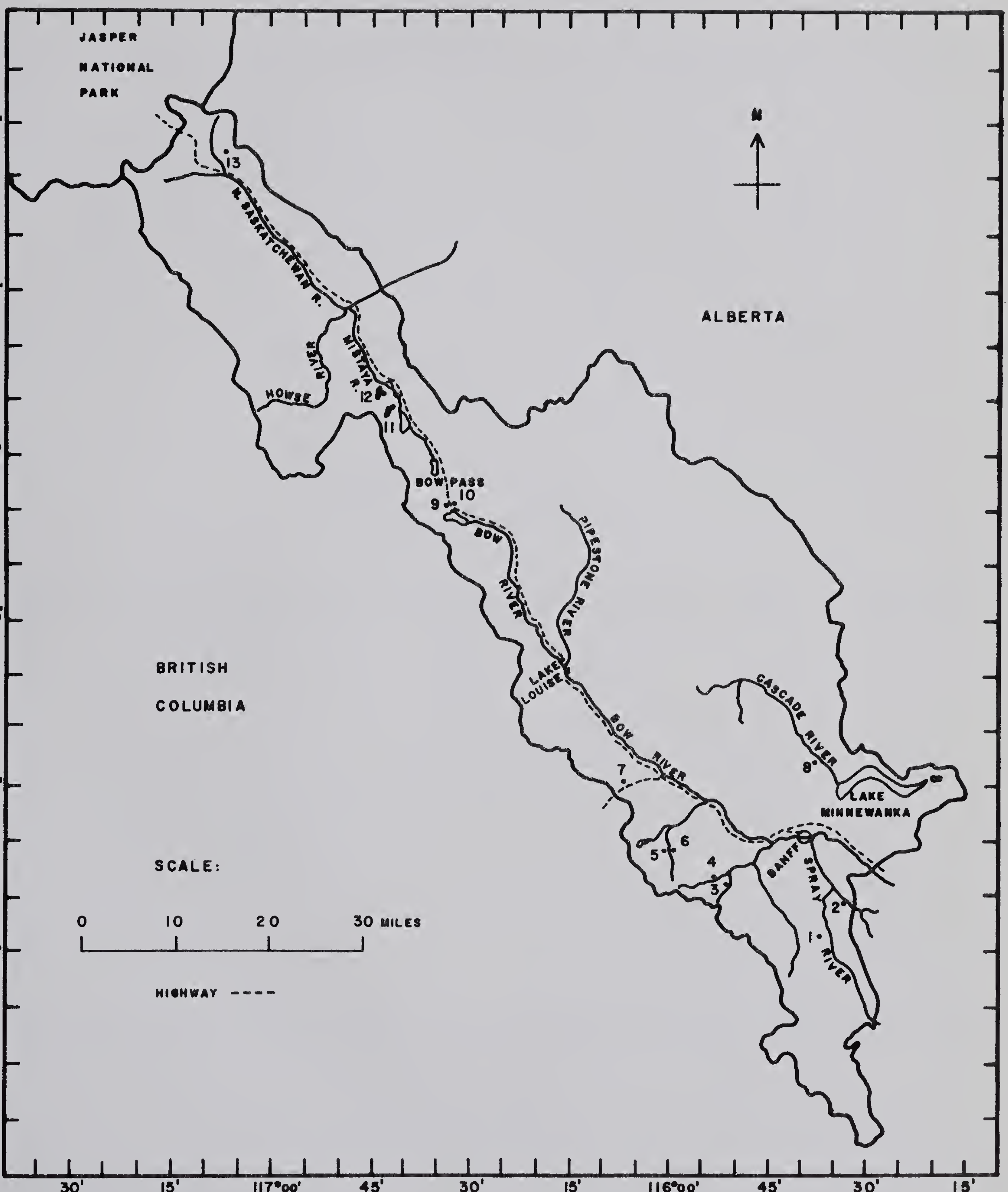
Selection and Location of Stands

Aerial photographs of the Department of Lands and Forests, Province of Alberta, (series, 160; scale, 1:40,000; date, 1950) of Banff and Jasper National Parks were examined in the lab and potential sampling sites selected. These sites were large in area, uniform in aspect and had slopes greater than 3°. Each potential site was then located and examined in the field and if it could satisfy the rest of the selection criteria, was used as a sampling area (stand).

An equal number of potential sites was selected for each of Banff and Jasper National Parks. However, after field examination it was found that most of the reasonably accessible potential sites in Jasper could not satisfy the selection criteria, thus only five stands were located in Jasper while 13 stands were located in Banff (Fig. 1 and 2; Appendix A, page 217). These stands were intensively studied during the summer of 1965.

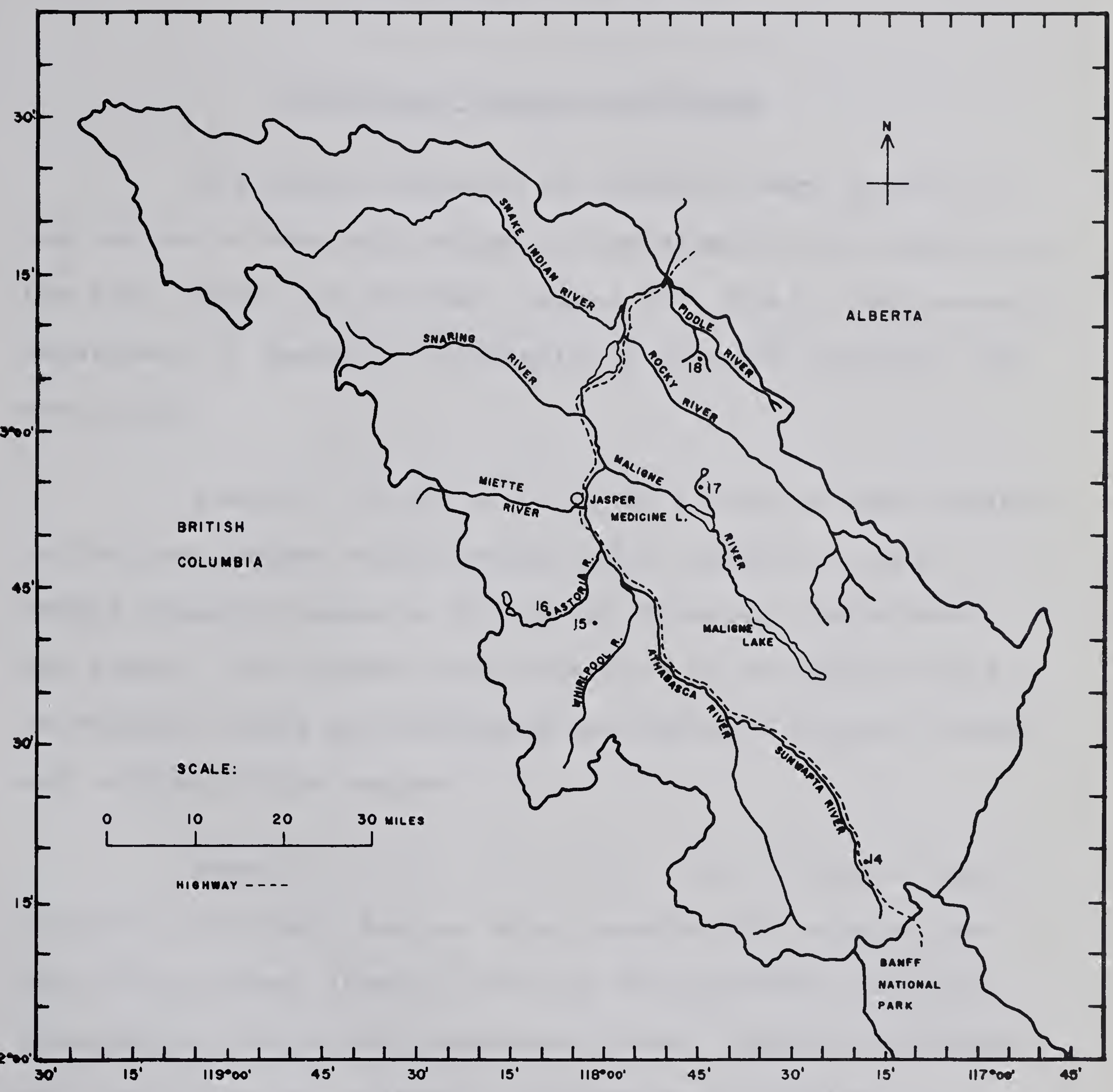
It is fair to say that the selection of stands for sampling was based on subjectively determined criteria. This action can be justified on the grounds that the research objective was to make a monographic study of a clearly defined statistical population.

Figure 1. Map of Banff National Park Showing the Locations of Stands 1 to 13 Inclusive



JASPER
NATIONAL
PARK
ALBERTA
BRITISH
COLUMBIA
N
N. SASKATCHEWAN R.
HOWSE
RIVER
MISTAYA R.
BOW PASS
BOW
RIVER
PIPESTONE RIVER
LAKE LOUISE
BOW RIVER
CASCADE RIVER
LAKE MINNEWANKA
BANFF
SPRAY
RIVER
1
2
3
4
5
6
7
8
9
10
11
12
13
SCALE:
0
10
20
30 MILES
HIGHWAY
15'
52°00'
45'
30'
15'
51°00'
45'
30'
15'
117°00'
45'
30'
15'
116°00'
45'
30'
15'

Figure 2. Map of Jasper National Park Showing the Locations of Stands 14 to 18 Inclusive



N
ALBERTA
BRITISH
COLUMBIA
SNAKE INDIAN RIVER
SNARING RIVER
FIDDLE RIVER
ROCKY RIVER
18
MALIGNE RIVER
17
MIETTE RIVER
JASPER
MEDICINE L.
ASTORIA R.
16
15
WHIRLPOOL R.
MALIGNE LAKE
ATHABASCA RIVER
SUNWAPTA RIVER
14
BANFF
NATIONAL
PARK
SCALE:
0 10 20 30 MILES
HIGHWAY ----
30'
15'
53°00'
45'
30'
15'
52°00'
30'
15'
119°00'
45'
30'
15'
118°00'
45'
30'
15'
117°00'
45'

IV UNDERLYING GEOLOGY OF STANDS, SUBALPINE SOILS AND SUBALPINE CLIMATE

Underlying Geology of Stands

The stands selected for sampling were located in two series of mountain ranges of the Alberta Rocky Mountains, the East Ranges and the Main Ranges (Dr. H.A.K. Charlesworth, Department of Geology, University of Alberta; personal communication).

Stands 1, 2, 3, 4, 5, 6, 8, 17 and 18 were located in the East Ranges which consist of a series of thrust-sheets exposing Mesozoic shales and Paleozoic carbonates and shales. The stands were underlain by Paleozoic rocks as Mesozoic rocks are recessive and underlie the low slopes and valleys of the region.

Stands 7, 9, 10, 11, 12, 13, 14, 15 and 16 were located in the Main Ranges which consist of a single complex thrust-sheet (Castle Mountain Thrust-Sheet) exposing Precambrian slates and sandstones, Lower Cambrian sandstones and quartzites and Paleozoic carbonates and shales.

Subalpine Soils

At the present time, there is no published description of the subalpine soils of Banff and Jasper National Parks. A report by Crossley (1951) on the

subalpine soils at Kananaskis, 30 miles east of Banff, appears to be the only detailed soil survey made in the subalpine zone. He found that Brown Podzolic, Grey Podzolic and Podzolic soils were the major soil types occurring on subalpine forested slopes in the region.

Subalpine Climate

The climatic data presented in Table 1 for Banff, Lake Louise and Jasper would no doubt have to be adjusted considerably to yield an accurate estimate of the climate as it exists at the higher elevations where the subalpine spruce-fir stands were located. The climatic data recorded at Lake Louise appear to be the closest available approximation to those which would be recorded in the subalpine, as Lake Louise is located at the lower boundary of the subalpine zone. The temperature and precipitation data are based on 30-year averages [(1931-1960); Temperature Normals for Alberta, 1964; Precipitation Normals for Alberta, 1965]. The length of the effective growing season (number of days with temperatures above 42° F) is based on a 10-year average [(1951-1960); Boughner 1964].

The mean annual temperature at Lake Louise is 31.9° F. The mean monthly temperatures are above 32° F for the months of April through October, the highest being 54.4° F in July and the lowest being 6.3° F in January. The maximum mean monthly temperature is 70.9° F in July

Table 1. Temperature and Precipitation Summaries and Effective Length of Growing Season for Banff, Lake Louise and Jasper

Temperature and precipitation data are 30-year averages (1931-1960); effective length of growing season is a 10-year average (1951-1960).

Recording Station	Mean Annual Temp (degrees F)	No. Months with Mean Temp Above 32° F	Max Mean Monthly Temp (degrees F)	Min Mean Monthly Temp (degrees F)	Effective Length of Growing Season (days)	Mean Annual Precipitation (inches)	Mean Annual Snowfall (inches)
*Banff	36.0	7	72.5	3.5	148	18.48	79.3
**Lake Louise	31.9	7	70.9	-6.5	-	30.37	193.3
†Jasper	37.8	7	73.6	2.0	157	15.98	49.2

*Elevation = 4853 ft above mean sea level
**Elevation = 5032 ft above mean sea level
†Elevation = 3480 ft above mean sea level

and the minimum mean monthly temperature is -6.5° F in January. The annual precipitation averages 30.37 inches and is evenly distributed throughout the year. The average annual snowfall is 193.3 inches occurring mainly in the months of October through May but snow has been recorded in every month of the year except July. The heaviest snowfall occurs in December at an average of 41.3 inches. Data on the length of the effective growing season for Lake Louise are not available but it is estimated that the length of the effective growing season would be less than two-thirds the 148 days recorded for Banff.

V FIELD METHODS USED IN VEGETATION ANALYSIS

Description of the Sampling Plot

"The need for quantitative records has made it necessary to give serious consideration to methods of sampling.... it becomes of prime importance to determine what constitutes an adequate sample in terms of the community as a whole and how to obtain such a sample with the minimum of effort." (Oosting 1956, page 32).

To fulfil the first objective of this study, it was decided that quantitative information on the vegetation structure and composition was essential. This made it necessary to select a standard sampling plot which could be used to sample the vegetation efficiently. Consideration was then given to the shape and size of sampling plot to be employed.

It was decided to utilize a square sampling plot (quadrat) despite the fact that Clapham (1932) and Bormann (1953) state that rectangular plots are usually more efficient for sampling. The choice of the quadrat as the basic unit was based on the following reasons: (1) the ease with which it could be laid out under field conditions; (2) a decreased edge effect which can often be a problem in using a rectangular plot if previous knowledge of the vegetation is not available; (3) results which could be

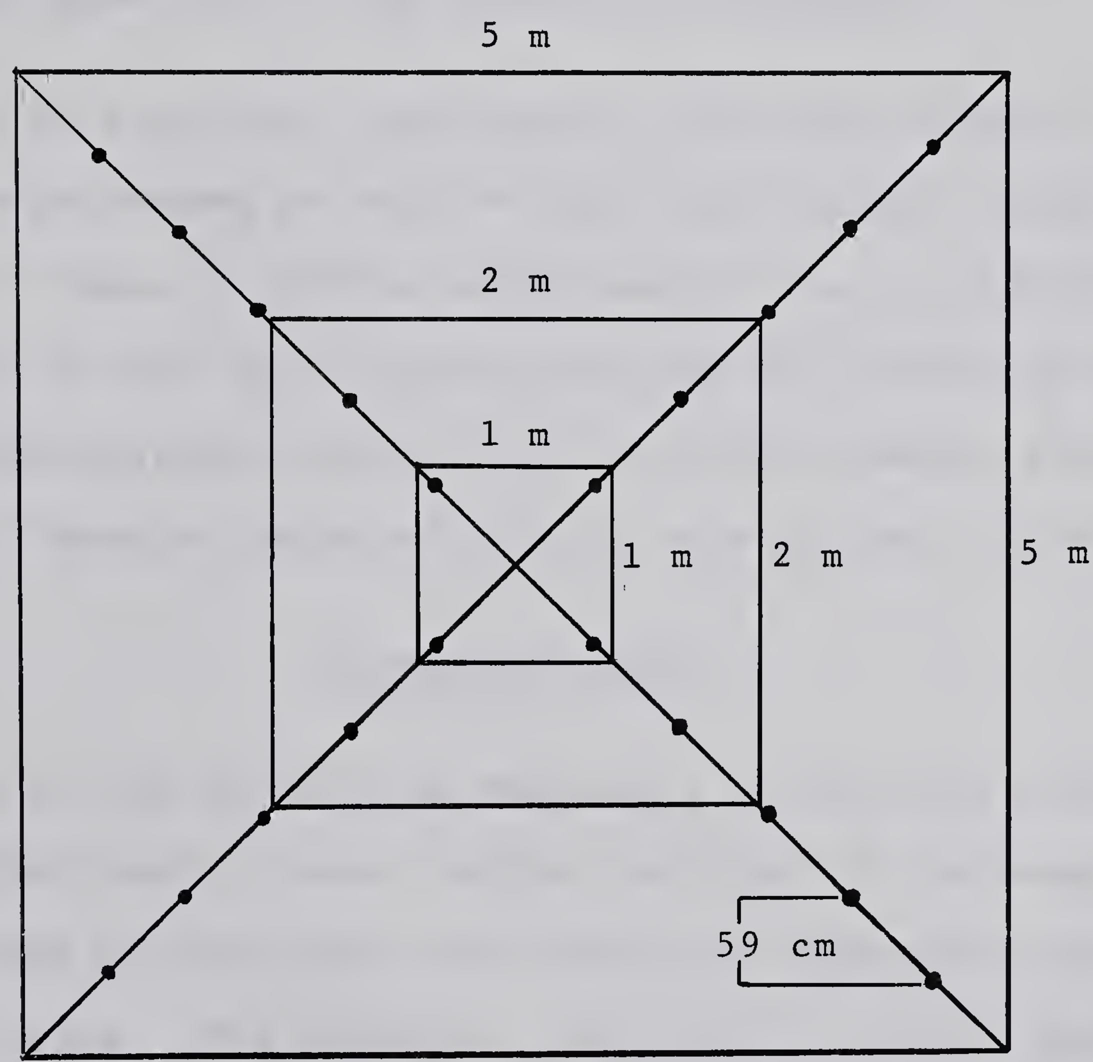
more easily compared with previous subalpine studies and other ecosystem studies in Banff and Jasper National Parks; (4) no previous knowledge of the vegetation pattern was available to indicate that a less standard shaped plot should be used.

The size of quadrat which should be used in any particular study will vary with the degree of homogeneity of the vegetation and the size and number of individuals composing the vegetation (Greig-Smith 1964, Chap. 2). Since the sizes of individuals vary with the different strata of a forest, it is not necessary to use the same size quadrat for each stratum, if it is assumed that the dispersion patterns of the strata are of a scale proportional to the relative sizes of their component individuals. It was therefore decided to use three quadrats of decreasing size to sample the tree stratum, shrub stratum and herb-dwarf shrub and bryophyte-lichen strata.

The tree stratum was sampled by a 5m x 5m quadrat enclosing a 2m x 2m quadrat in which the shrub stratum was sampled. Within the 2m x 2m quadrat a 1m x 1m quadrat was located in which the herb-dwarf shrub and bryophyte-lichen strata were sampled. The three quadrats had a common centre point (Fig. 3). A quick and efficient method of laying out the quadrats was utilized in the field. Four lengths of nylon cord were fastened together and distances corresponding

Figure 3. Diagram of Sampling Quadrats Used in Vegetation Analysis

Diagonal lines represent quadrat cords (page 32); the points on diagonals represent cover sampling points (page 34).



to half the diagonal lengths of each quadrat were marked on the cords, with the origin being the point at which the cords were fastened. Then by securing the origin of the quadrat cords and stretching them to form four 90° angles, the diagonals of the three quadrats were laid out. The quadrats were always laid out in the field so that two of their sides were parallel to the elevation contours.

Five points, equidistant from each other (59 cm apart), were marked on each of the four quadrat cords (Fig. 3). These 20 points were used in the quantitative assessment of the cover (proportion of the ground occupied by perpendicular projection onto it of the aerial parts of plants) of species populations and vegetational strata.

Sampling Scheme

It was considered desirable to utilize a sampling scheme which would insure random location of the sampling quadrats and at the same time facilitate adequate sampling of large areas. The essential features of random sampling are: (1) every unit of a population has an equal and independent chance of being represented in the sample and, therefore, the observed variance of the data can be used as the basis of tests of significance; (2) the elimination of biased information, which is a problem when systematic methods (quadrats spaced at equal distances) are used if the vegetation pattern is not random (Schumacher 1954,

Chap. 4); (3) The information gained can be subjected to statistical tests as most parametric statistics are based on random samples of populations. Randomization may be restricted in any way such that these features are still true. Thus, if a sampling area is stratified into a number of blocks and each one sampled randomly, no loss in the precision of the results is observed (Bourdeau 1953; Schumacher and Chapman 1954, Chap. 4).

A form of stratified random sampling was employed in this study. Following a compass bearing, a sampling line crossing the elevation contours was run through the centre of the stand. Sampling points were located along this line either at 50-ft elevation intervals or distances of 100 m, whichever occurred first. Quadrats were placed at the ends of reference lines measured out along the contours from each sampling point. The length of the reference lines was determined by consulting a random numbers table with the maximum set at 50 m. The reference line was measured to the right of the sampling line if the number was odd and to the left if the number was even. Sampling lines were run normal to the elevation contours instead of along them in order to obtain a representative sample of the subalpine forest, which occupies a specific altitudinal range (Introduction, page 1).

This sampling procedure was continued until the

desired level of accuracy was reached. The level of accuracy was set, in accordance with other ecosystem studies in Banff and Jasper National Parks, at a standard error of 10% of the mean density per quadrat of all the trees and 15% of the mean density per quadrat of the most common tree species in the stand (Schumacher and Chapman, Chap. 2). If tree limit [lower boundary of Krummholz zone (Hustich 1952)] was reached before the level of accuracy requirement was satisfied, a new sampling line was started 150 m to the right or left, as determined by reference to the random numbers table, of the original line and sampling was continued, going down slope in the same manner as before.

Since spruce-fir forms an extensive forest in the Rocky Mountains, it was difficult to accurately delimit stands and thus sampling intensity (i.e., area of sampling plots expressed as a percentage of stand area) was often infinitesimally small.

Sampling Procedure for Each of the Strata

Tree Stratum
(5m x 5m quadrat)

(1) Density

All trees (stems over 3 inches dbh) rooted in the 5m x 5m quadrat were counted by species and separate records kept for living and dead individuals. Similar counts were

made for saplings (stems 1 to 3 inches dbh).

(2) Diameters of Trees

The diameters of all stems over 3 inches dbh were recorded by species in the 5m x 5m quadrat using either Swedish tree calipers or a Lufkin tree tape. The diameters of living and dead trees were recorded separately.

(3) Basal Area (cross sectional area of stems greater than 3 inches dbh)

Basal area of all trees was recorded by species for living and dead individuals, using the "variable-radius" sampling method introduced by Bitterlich (1948; see Grosenbaugh 1952). The centre point of the 5m x 5m quadrat was used as the sampling point. The Bitterlich sighting prism was then used to count those trees that were within a distance from the sampling point of not more than 33 times their stem diameter. This ratio is so fixed that the count at the point multiplied by 10 corresponds directly to square feet of basal area per acre.

(4) Tree Canopy Cover

(a) An estimate of tree canopy cover was obtained at each of the 20 cover points marked on the diagonals of the 5m x 5m quadrat by looking directly up at each point and recording presence or absence of foliage above the point (same observer for all estimates). The points having foliage present were totalled for the whole stand and expressed

as a percentage of the total points to give a measure of canopy cover.

(b) A second measurement of canopy cover was obtained by a photographic method. A Kodak Starflex camera, using Kodak 127 black and white film, was placed on the ground at the centre of each quadrat and levelled. A photograph was then taken looking up at the tree canopy. The film was interpreted in the laboratory.

(5) Increment Cores from Trees

To learn something about stand history, ages and longevity of tree species, a series of increment cores was taken from the upslope side of trees of representative size classes. The heights and diameters at breast height were recorded for each tree bored. The trees so treated did not necessarily have to occur in a 5m x 5m quadrat.

Shrub Stratum

(2m x 2m quadrat)

(1) Density

Tree transgressives (individuals 12 inches tall to 1 inch in dbh) were counted in the 2m x 2m quadrat and the densities recorded by species. Densities were recorded for each shrub species and layering fir by estimating the number of stems rooted within the boundaries of the 2m x 2m quadrat.

(2) Height of Individuals

The heights of all shrubs and transgressives (up to 6 ft) occurring in the 2m x 2m quadrat were measured in inches. For transgressives which were taller than 6 ft, a subjective estimate of their height was made.

(3) Cover

Cover estimates for shrubs, layering fir and tree transgressives were done at each of the 20 cover points marked on the diagonals of the 5m x 5m quadrat (Fig. 3, page 33). The point quadrat method of estimating cover was employed (Warren Wilson 1959). A no. 14 (fine) knitting needle was lowered through the vegetation at each cover point and every species which made contact with the tip of the needle, as it was being lowered, was recorded by name. A cover value was obtained for a species by summing its contacts and expressing them as a percentage of the total cover points in the stand.

Herb-Dwarf Shrub Stratum

(1m x 1m quadrat)

(1) Density

The number of spruce and fir seedlings (individuals less than 12 inches tall) was recorded in each quadrat. Density was not noted for any other member of this stratum because of the difficult and often impossible task of defining countable individuals.

(2) Frequency

Every species occuring in a 1m x 1m quadrat was recorded by name. Unknown species in the quadrats were assigned descriptive names and then collected for later determinations.

(3) Cover

Cover estimates were obtained for herb and dwarf shrub species using the point quadrat method described for the shrub stratum (page 39).

Terrestrial Bryophyte-Lichen Stratum

Frequency and cover estimates for terrestrial bryophytes and lichens were obtained by the methods used in the herb stratum. All unknown bryophytes and lichens were collected for later determinations by the appropriate systematists.

Presence List, Collections and Subjective Estimates

After the quantitative sampling was completed, a thorough survey was made in the stand to compile a complete presence list which would include species not appearing in the quadrats. Unknown species in the stand were collected and preserved for later identification.

A sample of 100 to 150 spruce cones was randomly collected in the stand and brought back to the laboratory for examination and the eventual determination of a hybrid index.

Lastly, subjective estimates of percentage cover, vitality, sociability and periodicity were made for each species. The semi-quantitative and qualitative scales used in these assessments followed Braun Blanquet (1932). The scales are given in Appendix B, page 218.

VI FIELD METHODS USED IN ENVIRONMENT ANALYSIS

To satisfy the second objective of this study, it was necessary to measure existing environmental features. Measurement of the complete "operational" environment (Mason and Langenheim 1957) of any area is time-consuming and expensive. Since both time and resources were limited in this study, it was necessary to select for measurement those environmental components which could be easily measured and at the same time could yield a composite picture of the general habitat of the stands. The environmental components measured can be divided into physiographic and edaphic variables.

Physiographic Variables

(1) Elevation

Elevation was measured at the centre of all sampling quadrats using a Taylor altitude barometer and recorded as feet above mean sea level. The elevation of the stand was taken as the mid-point of the elevation range traversed.

(2) Slope Angle

Slope angle measurements were taken at all quadrats using a Blume Leiss altimeter. The general slope angle of the stand was taken as the mean value of these spot readings.

(3) Slope Aspect (Slope Exposure)

Slope aspect readings were obtained at all quadrats by sighting a compass bearing along the fall line of the slope. The readings were recorded in degrees, east or west of the two cardinal points of the compass.

(4) Light Intensity

Spot light intensity readings were taken at random throughout the stand using a Weston Master IV exposure meter. Light intensity was also measured at points outside the stand. All readings were taken as close as possible to mid-day. Mean light intensity inside the stand was expressed as a percentage of mean light intensity outside the stand to give a comparable estimate for each stand.

Edaphic Variables

(1) Soil Temperature

Soil temperature measurements were taken at a depth of 6 inches in all quadrats using a Taylor mercury-actuated dial probe thermometer.

(2) Soil Pit

One soil pit was dug in the stand. The profile of the pit was examined and the existing horizons described according to color and texture. The thickness of each horizon was measured in inches. One soil sample was collected from each horizon and brought back to the laboratory for analysis.

Observations on root distribution were made noting the depth at which maximum root penetration occurred.

VII LABORATORY METHODS APPLIED TO FIELD DATA

Tree Canopy Cover Photographs

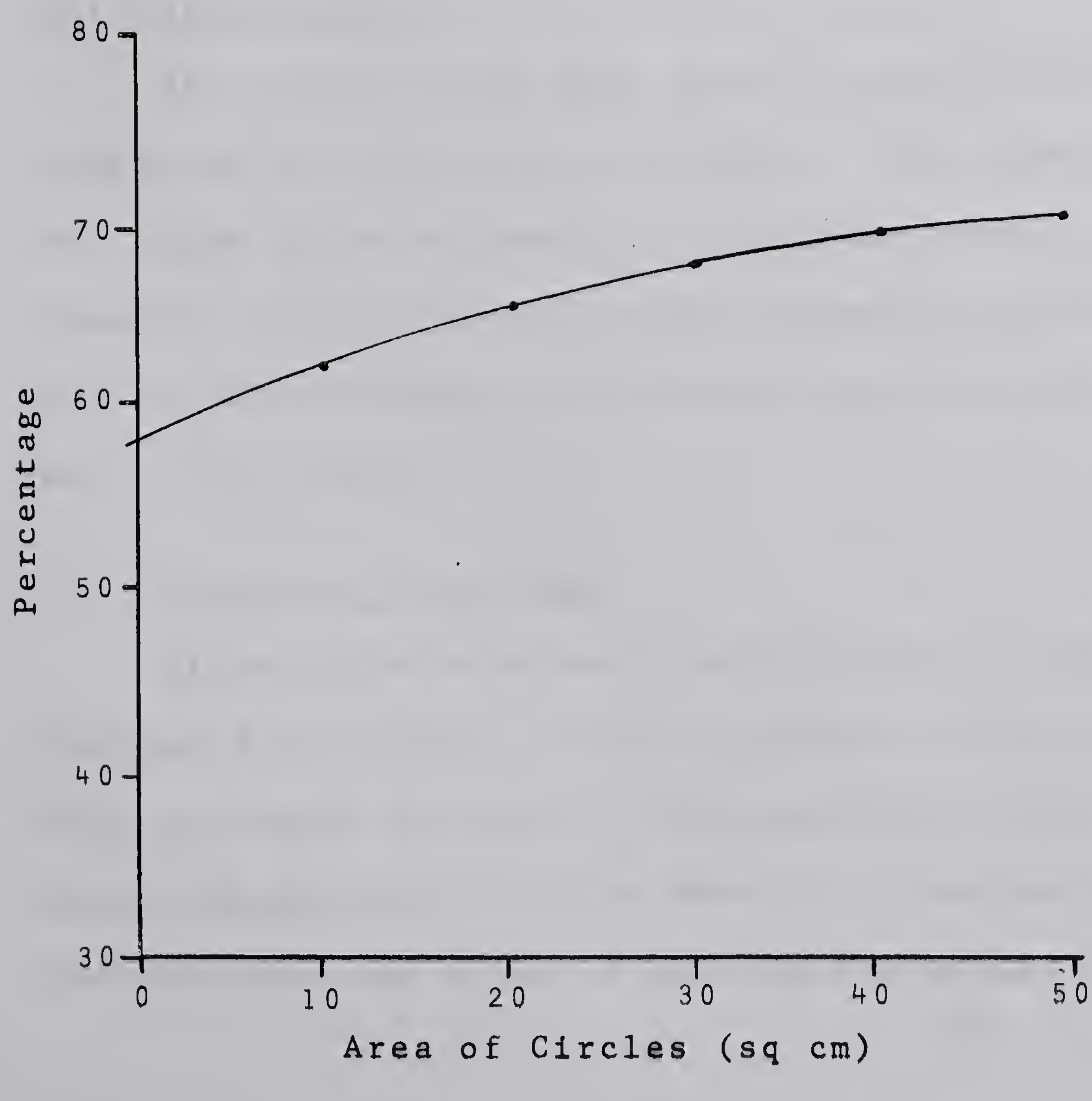
Tree canopy cover photographs (page 38) were examined and an estimate of cover obtained by a modification of the point quadrat sampling method. It was recognized that the most accurate representation of canopy cover on the photograph was at the centre and that because of the lens angle, distortion of actual cover increased towards the edge of the picture. A method was devised which would take this into account.

Five concentric circles of equally increasing area were marked on an acetate paper template. Sampling points were marked equidistant from each other within each circle. The innermost circle contained 10 points and each successively larger circle contained 10 more points than the previous one. The template was then placed over the photograph and presence or absence of foliage recorded for points within the circles [Fig. 4 (a)]. Presence of foliage was expressed as a percentage of total points for each circle on a per stand basis. The results were graphed on two-dimensional graph paper with the abscissa representing the areas of the circles and the ordinate representing the percentage cover [Fig. 4 (b)]. The resulting curve was extended across the ordinate and the point of intersection

Figure 4 (a). A Typical Canopy Cover Photograph with Sampling Points Marked on It

Figure 4 (b). Diagram Showing Graphical Method of Obtaining "Corrected" Estimate of Tree Canopy Cover

Stand 4 is used as a representative stand.



80
70
60
50
40
30
Percentage
0
10
20
30
40
50
Area of Circles (sq cm)

taken as the "corrected" estimate of percentage tree canopy cover at any point in the stand.

Stand History from Increment Cores

Every stand has its own peculiar history, a major variable which is often overlooked in ecological comparisons (Horton 1956, 1959; La Roi 1964). Correlation attempts between environmental and vegetational variables would be pointless without an estimate of stand age, as both vegetation pattern and species composition depend on the length of time the area has been available for colonization and growth (Cain 1939; Horton 1956).

(1) Oldest Tree

Ring counts were made on all cores and the results expressed as age at breast height. The oldest core counted was taken as an estimate of the maximum age of the stand. However, as many of the larger trees were decayed at the centre, the maximum age estimate may not be the true maximal of the stand.

(2) Practical Stand Age

Since all stands were uneven-aged, it was considered desirable to obtain a single synthetic figure which would best represent the age of the stand as a whole. Practical stand age was taken as the mean of: the maximum stand age; the dominant age group of spruce; the dominant age group of

fir; and the mean age of all the cores.

(3) Environmental Disturbances

The cores were also examined for growth suppressions which could be attributed to environmental causes. Many cores showed suppressions which were attributable to defoliation by insects, wind action or severe climatic disturbances. No attempt has been made to use this information in the vegetation-environment correlations.

Hybrid Index

The spruce portion of the climax subalpine spruce-fir forest in Alberta is composed of a complex of two species, *Picea glauca* and *Picea engelmannii* (Horton 1959). In the process of introgressive hybridization, there is repeated back-crossing of the hybrids with the parents and thus individuals may vary, morphologically, all the way from typical white to typical Engelmann spruce.

To establish the morphological position of the spruce fraction of each stand, a hybrid index was developed using the method of Horton (1959). Five possible categories were used ranging from typical white spruce, through three intermediate classes to typical Engelmann spruce. The criteria used in differentiating the categories were in the cone scales.

The following description of the scales of the two

species and their intermediates follows that of Horton (1959). White spruce has scales which are stiff, entire and rounded at the apex with the widest part one-third (of the total length) back from the apex. Engelmann spruce has scales which are thin, wavy, erose of margin and narrow or wedge-shaped at the apex with the widest part close to the middle. Also, white spruce customarily has rounded-tipped bracts, whereas, Engelmann spruce has accuminate-tipped bracts. The half-way intermediate represents a compromise of the above characteristics, usually having a broad scale with an ovate apex, more-or-less serrated and sometimes wavy. Then there are the intermediates inclined towards white or Engelmann spruce which possess some typical and some hybrid features.

The cones collected (field method, page 40) in each stand were categorized according to their cone scale characteristics and then, for an evaluation of degree of hybridity of a stand, an index was devised by assigning values to the five categories ranging from zero for pure white spruce to four for pure Engelmann spruce. The percentages of the total cone sample represented by each category were calculated; these, weighted by the appropriate value and summed, gave the hybrid index for a stand. According to this method, the index has a range from zero for pure white spruce to 400 for pure Engelmann spruce.

It should be emphasized that with introgression occurring, pure stands of Engelmann spruce are difficult to find and thus the extreme value of 400 does not really apply. There are, however, relatively typical stands and the index is useful for indicating these (Horton 1959).

Plant Identifications and Nomenclature

Unknown vascular plants collected in the field were identified using "The Flora of Alberta" (Moss 1959). Nomenclature follows the same reference. Bryophyte and lichen collections were identified by Dr. C. D. Bird of the University of Calgary. Nomenclature of mosses follows that of "A Preliminary Flora of the Alberta Sphagna and Musci" (Bird 1964). Nomenclature of liverworts follows that of "Boreal Hepaticae; A Manual of the Liverworts of Minnesota and Adjacent Regions" (Schuster 1953). Nomenclature of lichens follows that of "A Catalogue of the Lichens Reported from Alberta" (Bird 1966). All plant collections are deposited as voucher specimens in the Herbarium of the Department of Botany, University of Alberta.

Physical and Chemical Properties of the Soil

Soil samples were analysed to obtain the following information.

Physical Properties

(1) Textural Analysis

Each soil sample was screened through a 2 mm screen and the less than 2 mm size fraction collected, weighed and expressed as a percentage of the total weight of the sample.

Mechanical analysis on the less than 2 mm size fraction of the mineral soils was done by the revised hydrometer method (Bouyoucos 1951) using a New Brunswick Scientific Company reciprocal shaker (Model R-7) to agitate the soil suspension. The textural classification followed was that of the United States Department of Agriculture (sand = 2.00 to 0.05 mm; silt = 0.05 to 0.002 mm; clay, less than 0.002 mm). This method was selected because of its simplicity and rapidity.

It should be noted that the hydrometer method does not call for the soils to be pretreated with HCl to destroy the carbonates and with H_2O_2 to destroy the organic matter. These materials are distributed and measured in the main group separates (Bouyoucos 1951).

(2) Moisture Parameters

(a) Field Capacity (Soil water content after gravitational water is drained away)

Field capacity was determined for each soil sample using the porous plate apparatus (U.S.D.A. Handbook 1954). Saturated samples were placed on the plate and allowed to

remain under a pressure of one-third of an atmosphere for 48 hr. The samples were then oven-dried at 105° C and the water content expressed as a percentage of the oven-dry weight of the soil.

(b) Permanent Wilting Percentage (Soil water content when plant leaves permanently wilt)

Permanent wilting percentage was determined for each soil sample using the pressure membrane apparatus with a cellulose casing membrane (U.S.D.A. Handbook 1954). Saturated soil samples were placed on the membrane and allowed to remain under a pressure of 15 atmospheres for 48 hr. The samples were then oven-dried and the water content expressed as a percentage of the oven-dry weight of the soil.

(c) Available Soil Water

The available water content of each soil sample was obtained by subtracting the permanent wilting percentage result from the corresponding field capacity.

Chemical Properties

(1) Available Nutrients

Each soil sample was analysed for concentrations of available nitrogen, available phosphorus and available potassium by the Agricultural Soil and Feed Testing Laboratory at the University of Alberta. The results were expressed

in pounds per acre. A subjective estimate of free lime content was performed on each sample at the time the nutrient analyses were done (all soils with the exception of two had no free lime).

(2) Soil Reaction (pH)

Soil reaction determinations were done on soil samples by the Agricultural Soil and Feed Testing Laboratory and expressed in the customary logarithmic form (pH); pH readings were later converted to hydrogen ion concentration to be used in vegetation-environment correlations.

(3) Soluble Salts (conductivity)

The conductivity of soil samples was measured by the Agricultural Soil and Feed Testing Laboratory to determine their soluble salt concentrations. All soil samples recorded negligible soluble salt effects.

VIII DESCRIPTION OF THE VASCULAR FLORA

Systematic Considerations

A total of 113 species, 79 genera and 29 families constituted the vascular flora of the 18 stands sampled.

Of the 113 species, six belonged to the tree stratum, 15 to the shrub stratum and 92 to the herb-dwarf shrub stratum.

The 79 genera occurred in the following proportions: four in the tree stratum; 13 in the shrub stratum and 62 in the herb-dwarf shrub stratum.

Of the 29 families, all but three belonged to the Subdivision Angiospermae. Only one family was represented in the tree stratum, eight occurred in the shrub stratum and 25 belonged to the herb-dwarf shrub stratum.

In terms of number of genera, the most important family was Compositae with 12 genera followed by Ericaceae and Rosaceae each of which had seven genera.

Presence

Presence Values were obtained for each species by expressing the number of stands of occurrence as a percentage of the total number of stands.

The distribution of the sampled flora into five Presence Classes (1-20%, 21-40%, 41-60%, 61-80%, 81-100%) suggests the floristic simplicity of the subalpine spruce-fir ecosystem (Fig. 5). Classes I and II (species which are rare and seldom present) contain 83 species, or 73% of the total flora, while Class V (species constantly present) contains only 10 species or 9% of the total flora. Only four species occurred in all 18 stands.

Constance

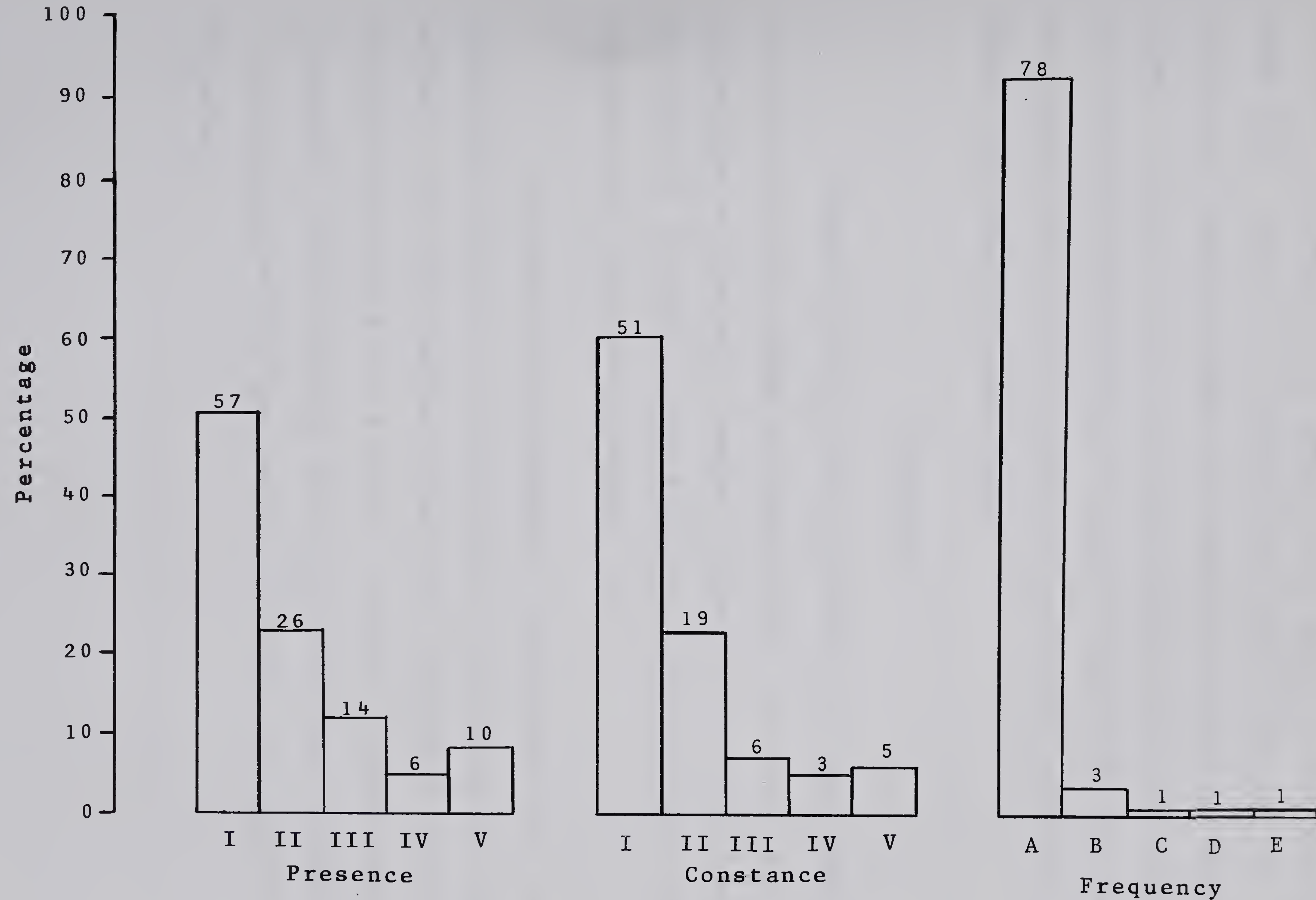
(Percentage occurrence within unit areas in the stands)

True Constance Values are not available as species lists for unit sampling areas in each stand were not obtained. The Constance Values used are based upon equal sampling areas for each of the comparable strata in the stands (500 sq m for tree species, 80 sq m for shrub species and 20 sq m for herb-dwarf shrub species).

The Constance diagram (Fig. 5) assumes the same form as the Presence diagram but gives a more accurate estimate of the number of truly characteristic species of the association since Constance is based on unit sampling areas in stands, whereas,Presence is based on entire stands of variable size. The data for the 18 stands yield a Constance list of 84 (Tables: 5, page 65; 7, page 68; 9, page 71) as compared to the 113 species of the Presence list

Figure 5. Diagrams of the Distribution of Vascular Species by Presence, Constancy and Frequency Classes

In each diagram the bars represent progressively higher percentage classes from left to right (1-20; 21-40; 41-60; 61-80; 81-100). The height of each bar represents the percentage of species which occurred in that class and the number of species is given at the top of each bar.


Percentage
100
90
80
70
60
50
40
30
20
10
0
57
26
14
6
10
I II III IV V
Presence
51
19
6
3
5
I II III IV V
Constance
78
3
1
1
1
A B C D E
Frequency

(Tables: 4, page 64; 6, page 67; 8, page 70 and Appendix C, page 220). This is a reduction of 26% imposed by the restricted areas on which the Constance determinations were based. Class V of the Constance diagram contains only 4% of the total flora making it apparent that very few species constantly occur in the subalpine spruce-fir ecosystem in Banff and Jasper National Parks.

Frequency

Frequency Values were obtained for each species by expressing the number of quadrats of occurrence as a percentage of the total number of quadrats in the 18 stands. The species involved in the Frequency determinations are the ones that form the Constance list.

The pattern of Frequency distribution (Fig. 5) emphasizes strongly the simplicity of the spruce-fir ecosystem. Only six species occur with a Frequency of greater than 20% (Classes B, C, D and E). Class A (1-20%) contains 78 species indicating that most of the species represented in the constance data are neither abundant nor regularly dispersed.

Presence Classification of the Vascular Strata

In the discussion of presence classification of the vascular strata, Presence Values of species will be indicated parenthetically following the species name.

Tree Stratum

Of the six species which occurred in the tree stratum, none had a Presence of less than 20% but only two had a Presence of greater than 80% (Table 2).

In Table 3 the tree species, all members of the family Pinaceae, are listed in order of decreasing Presence. The two dominants, *Picea engelmannii* (100) and *Abies lasiocarpa* (100), recurred consistently. *Pinus albicaulis* (44) and *Pinus contorta* var. *latifolia* (39) occurred in less than one-half of the stands. *Larix lyallii* (22) and *Picea mariana* (22) were found in less than one-fourth of the stands.

Shrub Stratum

Ten of the 15 species considered to belong to the shrub stratum had Presence Values of over 20% and one had a Presence of greater than 80% (Table 2).

Presence Values for shrubs are given in Table 18, page 116. On the basis of Presence alone the most important species are: *Salix drummondiana* (89), *Menziesia glabella* (78),

Table 2. Presence Class Distribution of Vascular Species by Strata

		Number of Species		
Class	Percentage	Trees	Shrubs	Herbs
I	0-20	0	4	53
II	21-40	3	5	18
III	41-60	1	2	11
IV	61-80	0	3	3
V	81-100	2	1	7
Total		6	15	92

Table 3. Presence Classification of the Tree Stratum

Species	Presence (%)
Picea engelmannii	100
Abies lasiocarpa	100
Pinus albicaulis	44
Pinus contorta	39
Larix lyallii	22
Picea mariana	22

Rhododendron albiflorum (61), Ledum groenlandicum (61), and Juniperus communis (50) all of which occurred in one-half or more of the stands.

Herb-Dwarf Shrub Stratum

Of the 92 species occurring in the herb-dwarf shrub stratum 39 had a Presence of over 20% (Table 2). The Presence Values of these species are given in Table 19, page 119. In terms of Presence only, the most important members of this stratum are: Pyrola secunda (100), Vaccinium scoparium (100), Moneses uniflora (94), Arnica cordifolia (94), Vaccinium membranaceum (89), Lycopodium annotinum (83) and Pyrola virens (83).

Geographic and Altitudinal Distributions of Vascular Species

As the study of the spruce-fir subalpine forest was conducted in two physiographic dimensions (i.e., through a latitudinal and elevational range), two floristic gradients resulted. The geographic (latitudinal range) and altitudinal (elevational range) gradients are by no means independent of each other. Because of the significant negative correlation between elevation and latitude ("r" = -0.5501 significant at the 2% level), the gradients are inversely related (i.e., a species which has a northern geographic distribution will have a low altitudinal distribution).

In view of the fact that these two apparently independent gradients actually form only one complicated floristic distributional pattern, an accurate method of depicting species distributions would be to plot each species on a separate scatter diagram with latitude represented on the abscissa and elevation on the ordinate. An alternative and simpler method is to use composite tables for the geographic and altitudinal distributions in which species presence is recorded against increasing latitude or increasing elevation. The second method has been employed in the following discussion because it not only gives the distributions of individual species but also shows the geographic and altitudinal variations in floristic composition of the ecosystem.

The geographic distributions (Tables: 4, page 64; 6, page 67; 8, 70) were prepared by arranging the stands in a south to north order and recording the presence of species in tabular form. Species of high Presence and occurring throughout the area were placed in the centre of the table and used as reference species. Then species having largely a southern distribution (recording 50% of their Presence in stands located south of the Bow Pass; Fig. 1, page 25), were arranged above the reference species in the order of decreasing northern distributional limits. Species exhibiting a northern distribution (50% Presence north of the Bow Pass) were arranged below the reference species in order

of decreasing southern distributional limits. In place of simple presence notations, quantitative values were used to indicate the abundance of species.

The altitudinal distributions (Tables: 5, page 65; 7, page 68; 9, page 71) were constructed in a similar manner to the geographic ones. Two hundred foot elevation classes, based on quadrat data, were arranged in order of increasing elevation and presence of species in the classes was recorded in tabular form. Species present throughout the entire 2,400 ft of elevation traversed during the study were placed in the centre of the table and used as reference species. Then species with a relatively low altitudinal distribution (recording 50% of their Constance at elevations below the mean elevation of 6,400 ft) were arranged below the reference species in order of decreasing upper elevational limits. Species having a relatively high altidudinal distribution (50% Constance above 6,400 ft) were arranged above the reference species in order of decreasing lower elevational limits. The number of quadrats in each elevation interval is given at the bottom of Tables 4, 6, 8. A true estimate of species occurrence in the elevation intervals of 7,200 to 7,400 ft and 7,400 to 7,600 ft was not obtained as the number of sampling quadrats falling into these classes was exceptionally low, six quadrats and two quadrats respectively.

The geographic distribution tables were formed from presence data and thus compose the Presence list referred to on page 57. The altitudinal distributions were based on quadrat data, so giving the Constance list referred to on page 55. Because these tables were designed to serve dual purposes (presence and constance lists plus species distributions), the geographic and altitudinal distributions of low Presence and low Constance species may tend to be overemphasized.

Tree Stratum

Engelmann spruce (Picea engelmannii) and subalpine fir (Abies lasiocarpa) occurred as constant associates throughout the entire latitudinal (Table 4) and elevational (Table 5) ranges. Geographically, lodgepole pine (Pinus contorta var. latifolia) and whitebark pine (Pinus albicaulis) were found sporadically throughout the region. On an elevational basis lodgepole pine showed largely a low altidudinal distribution (centre of concentration below 6,200 ft), whereas, whitebark pine never occured at elevations below 6,400 ft. Alpine larch (Larix lyallii) occurred only in the southern parts of the study area (Stands 1, 3, 5, 7; Fig. 1, page 25; Table 4) and at correspondingly high elevations (over 7,000 ft, Table 5). In contrast, black spruce (Picea mariana) was found exclusively in the northern sector (Stands 14, 15, 16, 17; Fig. 2,

Table 4. Geographic Distribution of Tree Species

Presence indicated by mean basal area estimates.
(P = present only)

Species	Stand Number																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Larix lyallii	P	-	4	-	4	7	-	-	-	-	-	-	-	-	-	-	-	-
Pinus contorta	-	15	-	-	-	8	7	6	-	-	-	-	-	4	-	7	6	-
Pinus albicaulis	P	P	-	22	-	-	P	-	-	-	-	-	P	-	P	2	P	-
Picea engelmannii	107	93	85	124	84	94	94	76	73	89	87	80	199	164	90	143	86	88
Abies lasiocarpa	53	48	59	34	87	51	38	54	72	79	80	85	61	19	72	58	35	130
Picea mariana	-	-	-	-	-	-	-	-	-	-	-	-	-	10	5	6	8	-

Table 5. Altitudinal Distribution of Tree Species

Species	Elevation in Feet Above Mean Sea Level												
	5200	5400	5600	5800	6000	6200	6400	6600	6800	7000	7200	7400	7600
Larix lyallii	-	-	-	-	-	-	-	-	-	X	-	X	
Pinus albicaulis	-	-	-	-	-	-	X	X	X	-	-	-	
Abies lasiocarpa	X	X	X	X	X	X	X	X	X	X	X	X	
Picea engelmannii	X	X	X	X	X	X	X	X	X	X	X	X	
Pinus contorta	X	X	X	X	X	-	-	-	X	X	-	-	
Picea mariana	X	X	X	X	X	X	-	-	-	-	-	-	
Number of Quadrats	24	24	29	56	37	32	48	57	34	20	6	2	

page 26; Table 4) and at relatively low elevations (below 6,400 ft, Table 5).

Shrub Stratum

Of the five shrubs which were present in more than 50% of the stands *Salix drummondiana* (89), *Menziesia glabella* (78), *Rhododendron albiflorum* (61) and *Juniperus communis* (50) occurred essentially in every part of the latitudinal range (Table 6). The first three of these species were represented in all elevation intervals up to 7,400 ft, a point above which no shrubs were found (Table 7).

Four species with a Presence of over 20% formed a recognizable species grouping; *Ledum glandulosum* (28), *Ribes viscosissimum* (44), *Lonicera involucrata* (39) and *Potentilla fruticosa* (28) occurred exclusively south of the Bow Pass (Fig. 1). The elevational distributions of these species with the exception of *Ledum* were high (centres of concentrations over 6,400 ft). *Ledum* was restricted to a mid-elevational range (5,600 ft to 6,600 ft).

Ledum groenlandicum (61) was the only species with a Presence greater than 20% that showed a northern geographic and low altitudinal (below 6,400 ft) distribution centre.

Shepherdia canadensis (33), occurred sparingly throughout the geographic range but exhibited a distinct

Table 6. Geographic Distribution of Shrub Species

Presence indicated by Prominence Values.
Prominence Value = $\sqrt{\text{frequency}}$ x absolute cover +1 (page 151).

Species	Stand Number																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Spiraea lucida	-	-	-	1.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ledum glandulosum	1.1	1.4	-	-	1.0	1.1	-	2.0	-	-	-	-	-	-	-	-	-	-
Ribes viscosissimum	1.0	1.0	1.2	1.1	1.4	1.0	1.1	1.0	-	-	-	-	-	-	-	-	-	-
Lonicera involucrata	-	1.0	-	1.2	1.0	1.1	1.0	1.0	-	1.0	-	-	-	-	-	-	-	-
Potentilla fruticosa	-	-	-	1.1	-	-	-	1.0	-	1.0	-	-	-	-	-	-	-	-
Rosa acicularis	-	1.0	-	-	-	-	-	1.0	-	-	-	-	-	1.0	-	-	-	-
Shepherdia canadensis	-	1.1	-	1.7	-	-	1.0	1.3	-	-	-	-	1.0	1.1	-	-	-	-
Ribes lacustre	-	-	-	1.0	-	-	-	-	-	-	-	-	-	-	-	1.0	-	-
Juniperus communis	-	1.1	-	1.1	-	1.2	1.0	1.1	-	-	-	-	1.0	1.1	-	1.6	1.2	-
Salix drummondiana	1.6	1.0	1.2	-	1.2	1.0	1.0	1.9	1.0	1.9	1.0	1.0	1.2	1.1	1.4	1.0	3.1	-
Menziesia glabella	22.	22.	1.0	1.0	1.1	3.1	42.	8.1	-	-	17.	4.8	-	-	3.5	1.5	36.	4.8
Rhododendron albiflorum	1.3	1.0	1.0	-	3.3	1.9	1.1	-	-	-	1.1	1.1	-	-	1.1	-	20.	7.1
Ledum groenlandicum	-	-	-	-	-	-	1.2	2.3	-	1.0	-	-	-	6.0	1.0	1.3	3.7	1.1
Betula glandulosa	-	-	-	-	-	-	1.0	1.1	-	-	-	-	-	-	-	1.0	1.1	-
Sorbus sp.	-	-	-	-	-	-	-	-	-	-	1.1	-	-	-	-	-	1.1	-

Table 7. Altitudinal Distribution of Shrub Species

Species	Elevation in Feet Above Mean Sea Level												
	5200	5400	5600	5800	6000	6200	6400	6600	6800	7000	7200	7400	7600
Spiraea lucida	-	-	-	-	-	-	-	-	X	-	-	-	
Potentilla fruticosa	-	-	-	-	-	-	-	X	X	-	-	-	
Lonicera involucrata	-	-	-	-	-	-	X	-	X	-	-	-	
Sorbus sp.	-	-	-	-	-	X	-	-	-	-	-	-	
Ribes viscosissimum	-	-	-	-	X	-	-	X	X	X	-	-	
Rhododendron albiflorum	X	X	X	X	X	X	X	X	X	X	X	-	
Salix drummondiana	X	X	X	X	X	X	X	X	X	X	X	-	
Menzieisa glabella	X	X	X	X	X	X	X	X	X	X	X	-	
Juniperus communis	-	X	X	X	X	X	-	X	-	X	-	-	
Ledum groenlandicum	X	X	X	X	X	-	-	X	-	-	-	-	
Shepherdia canadensis	X	X	X	-	-	-	-	X	-	-	-	-	
Ledum glandulosum	-	-	X	X	X	X	X	-	-	-	-	-	
Betula glandulosa	-	-	-	X	X	-	-	-	-	-	-	-	
Number of Quadrats	24	24	29	56	37	32	48	57	34	20	6	2	

low altitudinal distribution (between 5,200 ft and 5,800 ft)

Herb-Dwarf Shrub Stratum

An examination of the geographic gradient (Table 8) shows that out of 92 species present only Vaccinium scoparium (100) and Pyrola secunda (100) occurred throughout the range.

Seven other high Presence species, together with the above constants, formed a consistently recurring group in the 18 stands (Table 8). In order of their geographic concentrations (south-north) they are: Vaccinium membranaceum (89), Moneses uniflora (94), Lycopodium annotinum (83), Phyllodoce glanduliflora (67), Phyllodoce empetriformis (56), and Pyrola virens (83). Six stands contained all nine species, in four stands one was missing, in five stands two were missing but in no stand were more than three species out of the group absent. Aside from this grouping of constant species no other obvious species aggregations occurred on a geographic basis.

Only Vaccinium scoparium, with a Constance Value of 100%, occurred in every elevation interval (Table 9). In the following discussion only, the numbers after the species names are Constance Values not Presence Values.

In addition to Vaccinium scoparium, seven other species of high Constance, five of them present in the

Table 8. Geographic Distribution of Herb-Dwarf Shrub Species

Presence indicated by Prominence Values.
Prominence Value = $\sqrt{\text{frequency}}$ x absolute cover + 1 (page 151).

Species	Stand Number																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Aster foliaceus	1.1	-	1.1	1.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Chimaphila umbellata	-	-	-	1.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cirsium sp.	-	-	-	1.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Elymus glaucus	-	-	-	1.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hedysarum sulphurescens	-	-	-	1.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hieracium sp.	-	-	-	1.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Osmorhiza purpurea	-	-	-	1.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Carex atrosquama	-	-	-	-	1.0	-	-	-	-	-	-	-	-	-	-	-	-	-
Saxifraga lyallii	-	-	1.1	-	1.0	-	-	-	-	-	-	-	-	-	-	-	-	-
Veratrum eschscholtzii	-	-	-	-	1.0	-	-	-	-	-	-	-	-	-	-	-	-	-
Epilobium hornemannii	-	-	-	-	1.0	1.1	-	-	-	-	-	-	-	-	-	-	-	-
Leptarrhena pyrolifolia	-	-	-	-	1.0	1.2	-	-	-	-	-	-	-	-	-	-	-	-
Petasites vitifolius	-	-	-	-	1.1	1.1	-	-	-	-	-	-	-	-	-	-	-	-
Luzula parviflora	1.1	-	-	-	1.1	1.0	-	-	-	-	-	-	-	-	-	-	-	-
Viola palustris	-	-	-	1.7	1.1	1.1	-	-	-	-	-	-	-	-	-	-	-	-
Castilleja miniata	-	-	-	1.1	-	-	1.0	-	-	-	-	-	-	-	-	-	-	-
Aster conspicuus	-	1.1	-	1.0	-	-	1.0	-	-	-	-	-	-	-	-	-	-	-
Vaccinium sp.	-	-	-	-	-	-	-	1.7	-	-	-	-	-	-	-	-	-	-
Mitella nuda	1.1	-	-	-	-	-	-	1.5	-	-	-	-	-	-	-	-	-	-
Equisetum palustre	-	-	-	-	1.1	1.1	-	1.0	-	-	-	-	-	-	-	-	-	-
Senecio lugens	-	-	1.1	-	-	-	1.0	1.0	-	-	-	-	-	-	-	-	-	-
Claytonia lanceolata	-	-	-	-	-	-	-	-	1.0	-	-	-	-	-	-	-	-	-
Ranunculus eschscholtzii	-	-	-	-	-	-	-	-	1.0	-	-	-	-	-	-	-	-	-
Viola orbiculata	-	-	-	-	-	-	-	-	1.0	-	-	-	-	-	-	-	-	-
Mitella pentandra	-	-	1.1	-	1.0	1.1	-	-	1.0	-	-	-	-	-	-	-	-	-
Carex franklinii	-	-	-	-	-	-	-	-	-	1.0	-	-	-	-	-	-	-	-
Pedicularis groenlandica	-	-	-	-	-	-	-	1.0	-	1.0	-	-	-	-	-	-	-	-
Carex concinnoides	-	-	-	-	-	-	1.1	1.0	-	1.1	-	-	-	-	-	-	-	-
Vaccinium myrtillus	-	-	-	-	-	-	-	-	-	-	1.3	-	-	-	-	-	-	-
Carex raymondii	-	-	-	-	-	-	-	-	-	1.3	-	1.1	-	-	-	-	-	-
Agoseris glauca	-	-	-	-	-	-	-	-	-	-	-	-	1.0	-	-	-	-	-
Trisetum spicatum	-	-	1.1	-	-	-	-	-	-	-	-	-	1.1	-	-	-	-	-
Achillea millefolium	1.0	-	-	1.1	1.1	1.1	-	-	-	-	-	-	1.0	-	-	-	-	-
Erythronium grandiflorum	-	-	1.0	1.0	-	-	-	1.0	1.0	-	-	-	1.1	-	-	-	-	-
Solidago multiradiata	-	-	1.0	1.1	-	1.0	1.0	-	-	-	-	-	1.0	-	-	-	-	-
Thalictrum occidentale	1.0	-	1.1	1.7	1.0	1.1	-	-	1.0	1.1	-	-	1.2	-	-	-	-	-
Zygadenus elegans	-	-	1.0	1.1	-	-	-	-	-	-	-	-	-	1.0	-	-	-	-
Arctostaphylos uva-ursi	-	-	-	1.1	-	-	-	1.0	-	-	-	-	-	1.0	-	-	-	-
Calypso bulbosa	-	1.0	-	-	-	-	-	1.0	-	-	-	-	-	1.0	-	-	-	-
Fragaria virginiana	1.1	-	1.1	2.0	1.0	1.0	1.0	1.0	-	1.1	-	-	2.1	1.0	-	-	-	-
Valeriana sitchensis	-	-	1.0	2.5	1.3	-	-	-	1.0	-	-	-	1.0	-	-	1.0	-	-
Senecio triangularis	-	-	1.0	1.3	1.0	-	-	-	-	1.0	-	-	-	-	-	1.0	-	-
Arnica rydbergii	-	-	1.1	-	-	1.1	-	-	-	-	-	-	-	-	-	1.0	-	-
Erigeron perigrinus	-	-	-	1.1	1.2	1.0	-	-	-	-	-	-	1.0	-	-	-	1.1	-
Stenanthium occidentale	-	1.1	-	1.1	1.1	1.0	1.0	1.1	-	-	-	-	-	-	-	-	1.1	-
Trollius albiflorus	-	1.0	1.1	-	1.1	1.0	1.0	-	1.0	1.1	-	-	1.1	-	-	-	1.0	-
Epilobium angustifolium	-	1.0	1.1	1.1	1.0	1.0	1.0	-	-	-	-	-	1.1	1.0	-	-	1.0	-
Aquilegia flavescens	-	1.0	1.0	1.1	-	-	1.0	-	-	-	-	-	1.2	-	-	-	1.0	-
Pyrola asarifolia	-	1.0	-	-	1.0	-	1.1	1.0	-	-	-	-	-	1.1	-	-	1.1	-
Antennaria racemosa	-	-	-	1.9	-	-	-	-	-	-	-	-	1.1	-	-	-	1.0	-
Goodyera repens	-	1.0	-	1.0	1.0	1.1	-	-	-	-	1.0	-	-	-	-	-	-	1.0
Vaccinium membranaceum	1.4	1.3	1.1	1.1	12.	2.5	4.2	3.1	2.6	1.1	4.1	2.1	-	-	2.7	2.8	7.6	9.0
Pyrola secunda	1.3	1.4	1.1	1.3	1.1	1.0	1.0	1.8	1.0	1.1	2.6	3.8	1.5	1.5	1.6	1.1	1.5	1.4
Vaccinium scoparium	18.	2.4	3.8	5.8	13.	20.	11.	6.1	18.	7.2	3.8	3.7	11.	1.1	8.2	9.7	5.1	1.3
Arnica cordifolia	1.1	1.1	1.5	2.7	5.5	2.2	1.1	1.1	1.0	1.0	-	1.0	7.0	1.0	1.0	1.1	1.9	1.1
Moneses uniflora	1.1	1.1	1.1	1.0	1.2	-	1.0	1.7	1.0	1.1	1.3	1.1	1.1	1.1	1.1	1.1	1.1	1.1
Lycopodium annotinum	1.0	-	1.0	-	1.1	1.1	1.0	1.1	-	1.1	6.8	12.	1.0	1.0	1.0	1.2	1.6	1.8
Phyllodoce glanduliflora	1.1	-	1.1	-	1.0	1.1	-	-	1.1	1.0	-	-	1.5	1.0	7.2	1.0	1.4	3.6
Phyllodoce empetriformis	1.1	-	1.0	-	1.1	1.0	-	-	8.0	1.1	-	-	1.0	-	1.1	1.0	-	1.1
Equisetum scirpoides	7.0	1.0	-	-	-	-	-	1.8	-	1.1	-	1.3	-	1.0	1.1	-	1.1	1.1
Polygonum viviparum	1.0	-	1.1	-	1.0	-	-	-	-	1.0	-	-	1.0	-	-	1.0	1.1	-
Cassiope tetragona	1.1	-	-	-	-	-	-	-	1.0	-	-	-	-	-	1.1	1.0	1.2	1.1
Pyrola virens	-	1.1	1.1	-	1.1	1.0	1.0	1.2	-	1.1	1.1	1.1	1.0	1.0	1.1	1.0	1.0	1.1
Linnaea borealis	-	3.1	-	1.5	-	-	1.2	6.6	-	-	1.1	-	-	2.9	-	1.4	1.8	1.2
Elymus innovatus	-	1.3	-	1.8	1.1	-	1.0	3.5	-	-	-	-	2.8	5.2	-	1.9	1.6	1.0
Cornus canadensis	-	-	1.1	-	-	1.1	1.1	5.4	-	-	1.0	1.5	-	-	1.0	1.7	2.2	1.2
Listera cordata	-	1.0	-	-	1.1	-	-	-	-	-	1.0	1.1	-	-	1.1	-	1.1	1.1
Caasiope mertensiana	-	-	1.0	-	1.2	1.0	-	-	2.0	1.0	-	1.0	1.0	-	3.1	1.0	-	-
Pedicularis bracteosa	-	-	1.1	1.0	1.1	-	1.0	1.0	1.0	1.1	-	-	2.1	-	-	1.0	1.1	1.1
Parnassia fimbriata	-	-	1.0	-	1.1	1.1	1.0	1.0	-	1.0	-	-	1.0	-	-	1.0	1.1	-
Oxyria digyna	-	-	1.0	-	-	-	-	1.0	-	-	-	-	-	-	1.0	1.0	1.0	1.0
Arnica latifolia	-	-	-	-	1.9	-	-	-	-	-	-	-	-	-	-	-	1.1	-
Deschampaia atropurpurea	-	-	-	-	1.1	-	-	-	-	-	-	-	-	-	-	-	1.0	-
Empetrum nigrum	-	-	-	-	-	1.2	1.2	1.1	-	1.0	-	1.0	1.1	1.0	1.0	1.4	1.5	1.0
Vaccinium vitis-idaea	-	-	-	-	-	-	1.0	1.4	-	1.0	-	-	-	1.7	-	1.0	1.1	1.1
Arctostaphylos rubra	-	-	-	-	-	-	1.0	1.0	-	-	-	-	-	1.0	-	-	1.4	-
Equisetum arvense	-	-	-	-	-	-	1.0	-	-	1.0	-	-	-	-	-	1.0	-	-
Carex concinna	-	-	-	-	-	-	-	1.1	-	-	-	-	-	-	-	1.0	1.1	-
Rubus pedatus	-	-	-	-	-	-	-	-	-	-	7.1	11.	-	-	1.2	-	1.1	1.2
Goodyera oblongifolia	-	-	-	-	-	-	-	-	-	-	1.0	1.0	1.0	-	-	-	-	-
Antennaria pulcherrima	-	-	-	-	-	-	-	-	-	-	-	-	1.0	-	-	-	-	-
Gentianella propinqua	-	-	-	-	-	-	-	-	-	-	-	-	1.0	-	-	-	-	-
Potentilla diversifolia	-	-	-	-	-	-	-	-	-	-	-	-	1.0	-	-	-	-	-
Pyrola minor	-	-	-	-	-	-	-	-	-	-	-	-	1.0	-	-	-	-	1.0
Astragalus frigidus	-	-	-	-	-	-	-	-	-	-	-	-	-	1.0	-	-	-	-
Lycopodium selago	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.0	-	-	-
Calamagrostis canadensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.1	-	-
Lycopodium alpinum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.0	-	-
Delphinium glaucum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.0	-
Dryas hookeriana	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.0	-
Hedysarum alpinum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.1	-
Artemisia norvegica	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.1

Table 9. Altitudinal Distribution of Herb-Dwarf Shrub Species

Species	Elevation in Feet Above Mean Sea Level 5200–5400	5400–5600	5600–5800	5800–6000	6000–6200	6200–6400	6400–6600	6600–6800	6800–7000	7000–7200	7200–7400	7400–7600
Deschampsia atropurpurea	-	-	-	-	-	-	-	-	-	X	-	-
Epilobium hornemannii	-	-	-	-	-	-	-	-	X	-	-	-
Leptarrhena pyrolifolia	-	-	-	-	-	-	-	-	X	-	-	-
Potentilla diversifolia	-	-	-	-	-	-	-	-	X	-	-	-
Carex raymondii	-	-	-	-	-	-	-	X	-	-	-	X
Arnica rydbergii	-	-	-	-	-	-	-	X	X	-	-	-
Carex concinnoides	-	-	-	-	-	-	-	X	-	-	-	-
Mitella pentandra	-	-	-	-	-	-	-	X	X	-	-	-
Chimaphila umbellata	-	-	-	-	-	-	-	X	-	-	-	-
Trisetum spicatum	-	-	-	-	-	-	-	X	-	-	-	-
Trollius albiflorus	-	-	-	-	-	-	-	X	-	X	-	-
Epilobium angustifolium	-	-	-	-	-	-	-	X	-	-	-	-
Solidago multiradiata	-	-	-	-	-	-	-	X	-	-	-	-
Goodyera repens	-	-	-	-	-	-	-	X	-	-	-	-
Thalictrum occidentale	-	-	-	-	-	-	X	X	X	-	-	-
Petasites vitifolius	-	-	-	-	-	-	X	X	X	-	-	-
Osmorhiza purpurea	-	-	-	-	-	-	X	X	-	-	-	-
Arnica latifolia	-	-	-	-	-	-	X	X	X	X	-	-
Zygadenus elegans	-	-	-	-	-	-	X	X	-	-	-	-
Antennaria racemosa	-	-	-	-	-	-	X	X	X	-	-	-
Equisetum palustre	-	-	-	-	-	-	X	-	-	-	-	-
Erythronium grandiflorum	-	-	-	-	-	-	X	X	-	-	-	-
Senecio triangularis	-	-	-	-	-	-	X	X	X	-	-	-
Achillea millefolium	-	-	-	-	-	-	X	X	X	-	-	-
Luzula parviflora	-	-	-	-	-	X	-	-	-	X	-	-
Vaccinium myrtillus	-	-	-	-	-	X	-	X	-	-	-	-
Aster foliaceus	-	-	-	-	-	X	X	X	X	-	-	-
Viola palustris	-	-	-	-	-	X	X	X	X	-	-	-
Valeriana sitchensis	-	-	-	-	-	X	X	X	X	X	-	-
Phyllodoce empetriformis	-	-	-	-	-	X	X	X	X	X	X	-
Cassiope mertensiana	-	-	-	-	X	X	X	X	X	X	-	-
Cassiope tetragona	-	-	-	X	-	X	-	-	-	X	-	-
Erigeron perigrinus	-	-	-	X	-	-	-	X	-	X	-	-
Aquilegia flavescens	-	-	X	-	-	-	X	X	X	-	-	-
Senecio lugens	-	-	X	-	-	-	-	-	-	X	-	-
Fragaria virginiana	-	-	X	-	-	X	X	X	X	X	-	-
Equisetum scirpoides	-	-	X	-	X	X	X	X	X	X	X	-
Phyllodoce glanduliflora	-	-	X	X	X	X	X	X	-	X	-	-
Vaccinium scoparium	X	X	X	X	X	X	X	X	X	X	X	X
Arnica cordifolia	X	X	X	X	X	X	X	X	X	X	X	-
Vaccinium membranaceum	X	X	X	X	X	X	X	X	X	X	X	-
Pyrola secunda	X	X	X	X	X	X	X	X	X	X	X	-
Moneses uniflora	X	X	X	X	X	X	X	X	X	X	-	-
Elymus innovatus	X	X	X	X	X	X	X	X	X	X	-	-
Lycopodium annotinum	X	X	X	X	X	X	X	X	X	-	-	-
Pedicularis bracteosa	-	-	X	X	-	X	X	X	X	-	-	-
Cornus canadensis	X	X	X	X	X	X	X	X	-	-	-	-
Linnaea borealis	X	X	X	X	X	X	X	X	-	-	-	-
Pyrola asarifolia	X	-	X	-	-	-	-	X	-	-	-	-
Empetrum nigrum	X	-	-	X	X	X	X	X	-	-	-	-
Pyrola virens	X	-	-	X	X	-	X	X	-	-	-	-
Listera cordata	-	X	X	X	-	-	X	X	-	-	-	-
Polygonum viviparum	-	X	-	-	-	-	-	X	-	-	-	-
Rubus pedatus	-	X	X	X	X	X	X	-	-	-	-	-
Artemisia norvegica	-	-	-	-	-	X	-	-	-	-	-	-
Mitella nuda	-	X	X	-	-	X	-	-	-	-	-	-
Oxyria digyna	-	-	-	-	X	-	-	-	-	-	-	-
Vaccinium vitis-idaea	-	X	X	X	X	-	-	-	-	-	-	-
Calamagrostis canadensis	-	-	-	X	-	-	-	-	-	-	-	-
Stenanthium occidentale	X	X	X	X	-	-	-	-	-	-	-	-
Hedysarum alpinum	-	-	X	-	-	-	-	-	-	-	-	-
Arctostaphylos rubra	-	-	X	-	-	-	-	-	-	-	-	-
Carex concinna	-	X	X	-	-	-	-	-	-	-	-	-
Calypso bulbosa	-	X	-	-	-	-	-	-	-	-	-	-
Aster conspicuus	X	X	-	-	-	-	-	-	-	-	-	-
Number of Quadrats	24	24	29	56	37	32	48	57	34	20	6	2

group of geographic constant species, occurred essentially throughout the entire elevational gradient. In order of their elevational concentrations (low to high), they are: Elymus innovatus (44), Moneses uniflora (78), Pyrola secunda (83), Vaccinium membranaceum (89), Arnica cordifolia (61), Phyllodoce glanduliflora (33) and Equisetum scirpoides (33).

Another 12 species with Constance Values over 10%, although not occurring over the entire elevational range, did tend to form recognizable species groups within definite elevational limits. In the order of increasingly lower elevational boundaries (Table 9) the groups are as follows:

Group One

Empetrum nigrum (28), Linnaea borealis (50), Cornus canadensis (44) and Lycopodium annotinum (50) were associated between the elevations of 5,200 and 6,800 ft. Empetrum was absent from two elevation intervals within the association range, and Lycopodium occurred in one higher elevation interval.

Group Two

Fragaria virginiana (33), Cassiope mertensiana (11), Phyllodoce empetriformis (33), and Valeriana sitchensis (11) occupied the elevational range of 6,200 to 7,200 ft. Fragaria and Cassiope each occurred in one lower elevation interval, while Phyllodoce was present in one elevation interval above

the group's upper limit.

Group Three

Achillea millefolium (17), Antennaria racemosa (11), Petasites vitifolius (11) and Thalictrum occidentale (28) were associated in an elevational range of 6,400 to 7,000 ft. No member of this group occurred in any other elevation interval.

On a geographic basis (Table 8) the distributions of the foregoing species groups could be summarized as: Group 1, continuous to slightly northern; Group 2, continuous to slightly southern; and Group 3, southern.

Finally, by examining Tables 8 and 9 together a similarity in the distribution of species is apparent. Twenty-five species occurred exclusively in stands located south of the Bow Pass (No. 1-10; Fig. 1, page 25; Table 8, page 70), whereas, only 14 species were found to be restricted to stands north of the Pass (No. 11-18; Fig. 1 and 2, pages 25 and 26). Accordantly, 24 species appeared solely at elevations greater than the mid-point of 6,400 ft and 12 species were confined to elevations below 6,400 ft (Table 9, page 71).

The distribution of species in the sampled subalpine spruce-fir stands can be summarized as a two-dimensional pattern controlled by the simultaneous effects of

latitude and elevation. Because of the correlation between latitude and elevation, both the geographic and altitudinal species distributions when taken independently contain information about the other (i.e., given a geographic species distribution the general elevational trends can be inferred and vice-versa).

IX STRUCTURAL DESCRIPTION OF THE SPRUCE-FIR ECOSYSTEM BY STRATA

Material presented in the previous chapter was qualitative in nature. The floristic composition of each vascular stratum was given along with percentage occurrences and distributional patterns of the vascular species. Thus far, nothing has been said regarding the structure of the strata. The following discussion is devoted to a quantitative description of the structural attributes sampled in each of the four strata.

Tree Stratum

Age of the Oldest Tree (age at breast height)

In all stands except No. 1 and 4 the oldest tree cored was an Engelmann spruce. Whitebark pine contributed the oldest cores in Stands 1 and 4 with ring counts of 353 years and 404 years respectively (Table 10). With the exception of Stand 10 all ages listed are actual ring counts. In Stand 10 a large Engelmann spruce (diameter = 23.6 inches), decayed at the centre, yielded a ring count of 385 years from 9 inches of a possible 12.3 inch core. Judging from the growth rate of the tree 70 rings were estimated to be contained in the missing 3.3 inches of core, so giving a conservative age estimate of 455 years.

The average age of the spruce-fir stands, as

Table 10. Estimated Values of Some Structural Attributes of the Tree Stratum

Stand No.	Age of Oldest Tree (years)	Practical Stand Age (years) [1]	Height of Tallest Tree (feet)	Spruce Hybrid Index [2]	Tree Canopy Cover (%)	Standard Dev. of Tree Canopy Cover	Coefficient of Dispersion [3]
1	353	195	65	323	35.0	16.7	**0.40
2	312	200	82	213	51.0	17.1	*0.57
3	346	234	89	337	62.0	14.7	**0.39
4	404	187	97	292	58.0	13.5	**0.38
5	352	222	89	316	43.3	10.9	**0.24
6	295	182	89	298	26.5	19.7	*0.63
7	300	239	97	269	50.0	18.9	*0.55
8	229	148	105	234	52.5	17.7	1.00
9	378	220	79	334	36.0	12.6	*0.67
10	†455	235	92	310	50.0	16.9	*0.69
11	460	240	107	337	60.0	9.3	*0.72
12	382	233	90	323	57.8	7.9	0.83
13	282	149	100	325	70.0	10.8	0.98
14	248	148	94	223	42.0	11.0	**0.29
15	345	195	97	274	34.0	18.3	*0.57
16	321	218	88	303	68.8	9.6	*0.56
17	224	158	83	265	30.3	19.6	**0.53
18	265	155	81	297	68.5	9.8	**0.48
Total:							
Mean	331	198	90	292	49.8	-	-
Standard Dev.	69.3	34.4	10.7	39.2	13.7	-	-

[1] For method of calculation see lab method, page 47
[2] For method of calculation see lab method, page 48; range is 0-400
[3] For method of calculation see text, page 80
† Estimated age (see text, page 75)
Departure from random dispersion towards regular dispersion significant at the 10% level = *, at 2% = **

determined from the age of the oldest trees, was 331 years. Stand 11 contained the oldest tree, a spruce of diameter 32.2 inches, which was counted at 460 years. The lowest age estimate was 224 years obtained from a spruce of diameter 16.3 inches in Stand 17.

Practical Stand Age

Practical stand age (lab method, page 47) is a synthetic figure representing the age structure of the stand as a whole and is thus much lower than the corresponding age determined from the oldest trees. The average age of the spruce-fir stands was calculated to be 198 years. Stand 11 was the oldest with an age of 240 years and Stand 8 was the youngest at an age of 148 years. The age-range (youngest to oldest) was thus 92 years.

Three age-groups were apparent amongst the 18 stands. Five stands were between the ages of 148 and 158 years, the age-range of 182 to 200 years also contained five stands and eight stands were from 218 to 240 years old. There was no apparent geographic trend of stand ages or age-groups. There was, however, some indication of an elevational stratification of age-groups. Group 1 (148 to 158 years) was composed of stands with elevations (mid-point of the elevational range traversed) below 6,000 ft. Stands of Group 2 (182 to 200 years) all had elevations between 6,300 ft and 6,800 ft. In Group 3 (218 to 240 years) stand

elevations were recorded ranging all the way from 5,900 ft to 7,000 ft. Five of the eight stands, however, had elevations between 6,700 ft and 7,000 ft.

None of the sampled spruce-fir stands were even-aged suggesting that no stand was started following a recent environmental catastrophe, such as fire. This suggestion is supported by data from the increment cores which showed no signs of severe fire damage in any stand.

<u>Height of the Tallest Tree</u>

In all stands Engelmann spruce trees were the tallest trees measured, ranging in height from 65 ft in Stand 1 to 107 ft in Stand 11 (Table 10, page 76). The average height of the tallest trees in the 18 stands was 90 ft. In six stands the tallest tree measured was also the oldest tree, indicating that spruce has the capacity for sustained height growth with increasing age.

<u>Spruce Hybrid Index</u> (range is 0 to 400)

The average spruce hybrid index (lab method, page 48) was 292 (Table 10, page 76) indicating that the spruce fraction of the sampled spruce-fir stands was composed of a hybrid swarm of intermediates (between white and Engelmann spruce) inclined towards pure Engelmann spruce. Seven stands had hybrid indices greater than 320 with the maximum value being 337 recorded in Stands 3 and 11. The spruce of

these stands can be considered as relatively typical Engelmann. The lowest hybrid index values were recorded in Stands 2 and 14 at 213 and 223 respectively. The spruce of these stands can be considered as half-way intermediates between pure Engelmann spruce and white spruce.

Spruce hybrid index was positively correlated with stand elevation ("r" = +0.5904; significant at the 2% level) indicating that as elevation increases, stands of more typical Engelmann spruce are found.

Tree Canopy Cover

The corrected tree canopy cover estimates (lab method, page 45) are listed in Table 10, page 76. The accompanying standard deviations show the "within-stand" variation of canopy cover as opposed to the "between-stand" variation given by the standard deviation at the bottom of the canopy cover column. The within-stand standard deviations are not directly related to the corrected cover percentages as they were computed from variations in percentage cover between photographs of each stand.

The mean tree canopy cover for the spruce-fir stands was 49.8% with a standard deviation of 13.7%. This between-stand variation is considerably less than some of the within-stand variations (Stand 6, SD = 19.7%; Stand 17, SD = 19.6%). The maximum canopy cover was recorded in

Stand 13 at 70% and a within-stand variation of 10.8%. Stands 16 (cover = 68.8%, SD = 9.6%) and 18 (cover = 69.5%, SD = 9.8%) also had relatively high canopy cover estimates. The minimum cover of 26.5% was obtained in Stand 6. Stand 7, with a cover estimate of 30.3%, contributed the next lowest canopy cover estimate.

The tree canopy cover estimates tend to disprove the commonly held assumption that spruce and fir form a continuous canopy composed of overlapping tree crowns and thus provide a within forest environment of deep shade in which only mosses and a few shade tolerant herbs exist.

<u>Coefficient of Dispersion</u> (Blackman 1942)

From the quadrat density data, coefficients of dispersion (variance:mean ratios) were calculated to show the distributional pattern of trees within the stand (Table 10, page 76). This is a within-stand arrangement of trees and is not to be confused with the two-dimensional species distribution referred to on page 73. The test makes use of the equality of variance and mean of the Poisson distribution. If the ratio of variance to mean is less than one, a regular distribution is indicated; if greater than one, a contagious distribution. The coefficients of dispersion were tested for significance by using the Index of Dispersion (Skellam 1952; David and Moore 1954).

$$\text{Index of Dispersion} = \frac{\text{variance } (N-1)}{\text{mean}}$$

where N-1 = the number of observations minus one

Significance is assessed from a Chi-square table, the observed index of dispersion being entered with degrees of freedom one less than the number of observations.

All stands with the exception of No. 8, 12 and 13 showed regular distributional patterns, seven of them significant at the 2% level (Table 10, page 76). The three exceptions had random distributional patterns.

The consistently regular distributional patterns of trees suggests: (1) competition for space between individual trees resulting in a structural homogeneity of the tree stratum; and (2) environmental factors vital to tree growth, for example, soil nutrients are uniformly dispersed in the sampled subalpine spruce-fir stands.

However, the validity of the information obtained from the coefficients of dispersion can be questioned, because as the density of individuals approaches the maximum possible density for the area (i.e., approaches the carrying capacity), the Poisson distribution no longer occurs (Greig-Smith 1964, page 60).

Density

The average density of living trees in the spruce-fir stands was 17.2 (expressed as density per 100 sq m throughout the discussion to follow). The highest density of 38 was recorded in Stand 18 (Table 11), a comparatively young stand (155 years) in which 80% of the trees were less than six inches dbh. Stand 7, a much older stand (239 years), had the lowest recorded density of 11.2. The density range for the 18 stands was 26.8. Excluding Stand 18, the remaining stands had remarkably uniform densities, with a mean value of 15.9, a standard deviation of 3 and a range of only 8.4.

The average density of standing dead trees, expressed as a percentage of the living trees, was 12% and in no stand was the percentage greater than 27%. There was a positive correlation ("r" = +0.5487; significant at the 2% level) between density of living and dead trees, which can be interpreted as meaning that with increasing density of trees, competition between individuals increases, resulting in a higher mortality of trees.

Basal Area

The highest basal area estimate of 260 (basal area expressed as square feet per acre throughout the discussion) was obtained in Stand 13 (Table 11) in which 63%

Table 11. Living and Dead, Density, Basal Area and Frequency Estimates for the Tree Stratum

Stand No.	Density (stems per 100 sq m)		Basal Area (sq ft per acre)		Frequency (%)	
	Living	Dead	Living	Dead	Living	Dead
1	15.6	1.6	159	9	100	35
2	15.8	1.4	155	10	100	25
3	14.4	2.8	147	22	100	35
4	16.6	1.8	178	19	100	30
5	16.8	2.4	174	26	100	45
6	15.4	1.6	160	15	100	20
7	11.2	3.4	138	35	100	45
8	16.1	2.8	136	7	90	30
9	16.4	1.8	145	5	100	15
10	17.8	1.2	168	11	100	30
11	16.4	3.0	167	10	100	50
12	17.4	1.0	165	6	100	25
13	19.4	0.8	260	17	100	15
14	19.6	1.4	196	9	100	30
15	13.4	1.6	167	7	100	25
16	16.4	2.0	215	14	100	35
17	12.0	0.4	134	4	95	5
18	38.0	5.0	217	29	100	55
Total:						
Mean	17.2	2.0	171	14	99	31
Standard Dev.	5.6	1.1	32.6	8.9	2.6	12.8

of the living spruce trees exceeded 12 inches bdh. The next highest estimate of 217 came from stand 18 which had the highest density. The lowest basal area estimate of 134 was made in Stand 17, which also had a relatively low density of 12 trees per 100 sq m. The observed range of basal area was 124 and the average was 171 for the 18 stands.

There was an expected positive correlation ("r" = +0.5788; significant at the 2% level) between tree canopy cover and basal area as these are similar measures; cover estimates the presence of aerial plant parts at a sampling point and basal area estimates presence of basal parts of a plant at a sampling point.

The average dead basal area expressed as a percentage of the living was only 8%, with a range from 3% in Stand 17 to 25% in Stand 7, which clearly indicates that no stand was in a state of decadency.

Frequency

Living trees occurred in 99% of the total 5m x 5m quadrats of the sampled spruce-fir stands. Tree frequency was less than 100% in only two stands. Stand 8, which showed a random distribution of trees (Table 11), had a frequency of 90%. A frequency of 95% was observed for Stand 17 which had a correspondingly low density estimate of 12 and basal area estimate of 134.

The average frequency of dead trees for the 18 stands was 31%, with a range from 5% in Stand 17 to 50% in Stand 11. Coefficients of dispersion (page 80) were not calculated for dead trees but from an examination of the density and frequency data it appears that dead trees were either randomly or regularly dispersed (i.e., high density stands had high frequencies and low density stands had low frequencies). This suggests that no environmental disturbances, resulting in the death of trees, occurred in localized areas of the stands.

Shrub Stratum

Woody individuals over 12 inches tall and tree reproduction (transgressives and layering fir) were classified as belonging to the shrub stratum. In the following discussion, "true" shrubs (individuals maturing in this stratum) and tree reproduction are treated separately. Density, cover and frequency estimates for shrubs and tree reproduction are given in Table 12.

Density

Shrub densities ranged from a practically negligible 0.6 (densities hereafter expressed as stems per 100 sq m) in Stands 9 and 13 to 731.3 in Stand 17, with an average density of 227.1.

The mean tree reproduction density was only 99.8,

Table 12. Density, Cover and Frequency Estimates for Total Shrubs and Tree Reproduction[1]

Stand No.	Shrubs: Density (stems per 100 sq m)	Shrubs: Cover (%)	Shrubs: Frequency (%)	Tree Reproduction: Density (stems per 100 sq m)	Tree Reproduction: Cover (%)	Tree Reproduction: Frequency (%)
1	420.0	28.8	100	172.5	22.0	80
2	380.0	27.0	95	37.5	5.3	45
3	16.3	1.5	85	260.0	39.0	95
4	53.8	3.0	45	23.8	8.3	30
5	97.5	8.3	55	67.5	18.5	70
6	97.5	9.3	60	42.5	10.0	45
7	430.0	50.0	90	60.0	13.8	60
8	658.8	22.8	62	96.3	15.5	34
9	0.6	-	5	236.3	38.3	80
10	22.5	3.5	55	203.8	38.3	95
11	486.3	17.8	80	16.3	16.3	30
12	151.3	7.0	40	25.0	14.0	60
13	0.6	0.8	50	75.0	17.0	60
14	137.5	7.5	65	120.0	10.3	40
15	122.5	6.8	45	170.0	30.8	85
16	67.5	4.8	45	106.3	16.0	45
17	731.3	71.0	100	20.0	8.5	30
18	213.8	15.0	75	50.0	9.8	45
Total:						
Mean	227.1	15.8	64	99.8	18.4	57
Standard Dev.	226.1	18.8	24.9	75.6	10.9	22.4

[1] Tree Reproduction = Transgressives and layering fir

less than one-half the equivalent shrub value. The highest density was recorded in Stand 3 at 260, and the next highest in Stand 9 at 236.3. Stands 11 and 17 had the two lowest densities, 16.3 and 20.0 respectively.

Cover

The average shrub cover of the spruce-fir stands was 15.8%. The highest recorded shrub cover of 71% occurred in Stand 17. The next highest, 50%, was found in Stand 7. Both of these stands had relatively low basal area estimates of 134 and 138 sq ft per acre respectively (Table 11, page 83). The remaining 16 stands had estimated cover values ranging from negligible in Stand 9 to 28.75% in Stand 1. There was a positive correlation between shrub densities and estimated cover values ("r" = +0.8536; significant at the 2% level).

Tree reproduction cover was more uniformly distributed among the 18 stands than shrub cover, with a range from 8.5% in Stand 17 to 39% in Stand 3. There was a positive correlation between reproduction densities and estimated cover values ("r" = +0.9016; significant at the 2% level).

The mean reproduction cover was greater than the mean shrub cover, whereas, mean reproduction density was considerably less than mean shrub density. This difference

is largely attributable to the habit of layering fir whose densely-leaved stems form a thick mat over the ground as opposed to the loose arrangement of the upright deciduous leaved stems of the shrubs, thus a higher cover per stem is recorded for fir than for shrubs.

Negative correlations between shrub and reproduction cover, and shrub and reproduction density were apparent. These correlations can be interpreted as meaning either: (1) a within-stratum competition between shrubs and tree reproduction resulting in the competitive exclusion of one or the other, or (2) that shrubs and tree reproduction have very different environmental requirements and habitats suitable for the growth and development of one will not support the other.

Frequency

Shrubs occurred in 64% of the 2m x 2m quadrats. The frequency range of shrub species was from 5% in Stand 4 to 100% in Stands 1 and 18.

Tree reproduction had a mean frequency of 57% with a range from 30% in stands 4, 11 and 17 to 95% in Stand 10.

Herb-Dwarf Shrub Stratum

All herbaceous plants and woody individuals under 12 inches in height were considered to belong to this

stratum. As for the shrub stratum, individuals maturing in the herb-dwarf shrub stratum are treated separately from tree reproduction (seedlings). Cover and frequency estimates are listed for herbs and dwarf shrubs along with cover, frequency and density estimates for seedlings in Table 13. Density was not obtained for other members of this stratum because of the difficulty in defining "countable" individuals.

Cover

The mean estimated cover value for herbs and dwarf shrubs was 25.6%. The highest cover of 39% was recorded in Stand 9, which had no measurable shrub cover (Table 12, page 86). Stand 2 had the lowest herb-dwarf shrub cover of 9% and a relatively high shrub cover of 27%.

This negative correlation between shrub and herb-dwarf shrub cover suggests: (1) a between strata competition in which a well-developed shrub layer prevents the growth and development of herbs and dwarf shrubs or (2) an environmental selection favouring either the growth of shrubs or herbs and dwarf shrubs.

The estimated cover values of seedlings were very low, the average being 0.8% with a range from 0% in Stands 3, 4 and 5 to 3.3% in Stand 12. There was no apparent correlation between seedling and herb-dwarf shrub

Table 13. Cover and Frequency Estimates for Herbs, Dwarf Shrubs and Seedlings and Density Estimates for Seedlings

	Herbs and Dwarf Shrubs		Seedlings		
Stand No.	Cover (%)	Frequency (%)	Cover (%)	Frequency (%)	Density (seedlings per 100 sq m)
1	30.3	95	0.3	15	75
2	9.0	75	0.5	15	60
3	5.8	80	0.0	20	30
4	21.0	100	0.0	20	95
5	36.8	100	0.0	25	70
6	25.8	100	0.5	20	45
7	17.8	95	0.3	10	25
8	37.4	90	2.1	52	390
9	39.0	80	0.5	45	95
10	13.3	75	0.8	25	130
11	29.3	95	1.0	40	80
12	37.8	100	3.3	35	285
13	34.5	100	0.5	40	620
14	10.3	85	0.8	15	45
15	32.0	95	1.0	30	760
16	21.0	85	0.3	25	250
17	34.5	100	1.3	40	205
18	25.0	95	0.8	50	390
Total:					
Mean	25.6	91	0.8	29	202.8
Standard Dev.	10.8	9.0	.82	13.0	209.9

cover most likely because of the limited available seedling data.

Frequency

Ninety-one per cent of the 1m x 1m quadrats were occupied by herbs or dwarf shrubs. Six stands had a frequency of 100% and the lowest frequency of 75% was recorded in Stands 2 and 10.

Seedlings had a much lower frequency, with a mean of only 29% and a range from 10% in Stand 7 to 52% in Stand 8.

Seedling Density

The highest seedling density was recorded in Stand 15 at 760 (hereafter expressed as density per 100 sq m) and the lowest in Stand 3 at 30. There was an observed mean density for the 18 stands of 202.8.

The high density estimates coupled with the relatively low frequencies, suggest that seedlings are highly aggregated in microenvironments within the stands which are favourable to seedling establishment.

Terrestrial Bryophyte-Lichen Stratum

Cover and frequency estimates for the bryophyte-lichen stratum are given in Table 14.

Table 14. Cover and Frequency Estimates for the Terrestrial Bryophyte-Lichen Stratum

Stand No.	Cover (%)	Frequency (%)
1	75.0	95
2	90.5	100
3	14.3	80
4	22.0	90
5	51.3	95
6	46.0	95
7	46.3	95
8	81.0	100
9	39.5	100
10	43.0	100
11	86.3	100
12	89.3	100
13	27.3	80
14	73.5	100
15	62.3	100
16	53.8	95
17	57.5	100
18	83.3	100
Total:		
Mean	57.9	96
Standard Dev.	23.8	6.4

Cover

The mean cover of the bryophyte-lichen stratum was 57.8%. In five stands bryophytes and lichens formed a continuous mat on the forest floor with estimated cover values over 80%, the highest being 90.5% in Stand 2. At the other extreme, bryophytes and lichens sometimes occurred only as localized patches with low cover. Stands 3 and 4 had the lowest estimated cover values of 14.3% and 22% respectively.

Frequency

Bryophytes and/or lichens were present in 96% of the 1m x 1m quadrats in the spruce-fir stands. Ten stands had frequencies of 100%; a frequency of 80% in stands 3 and 13 was the lowest recorded.

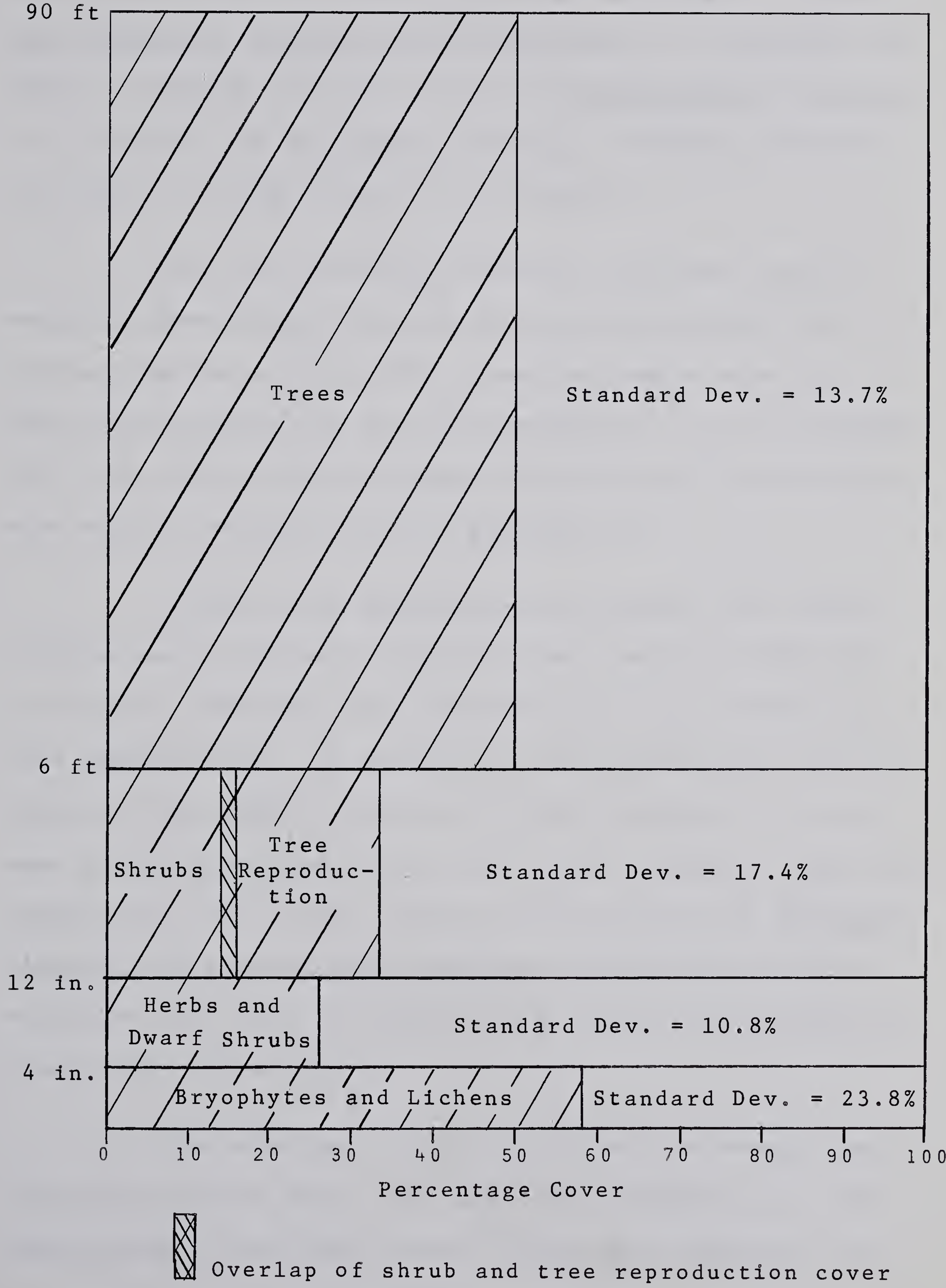
Cover-Stratification of the Spruce-Fir Ecosystem

The quantitative relationships between the four strata of the subalpine spruce-fir ecosystem become apparent in a cover-stratification diagram (Fig. 6). This diagram is based on the mean cover values of each stratum. The heights are the estimated maximal stratal heights with the exception of the tree stratum which is the average height of the tallest trees (Table 10, page 76).

The bryophyte-lichen stratum is the best-developed

Figure 6. Cover-Stratification Diagram of the Subalpine Spruce-Fir Ecosystem

Stratal heights are not drawn to scale.



of the four strata with a mean cover estimate of 57.8%. Populations of four mosses, Hylocomium splendens, Pleurozium schreberi, Ptilium crista-castrensis and Dicranum scoparium, together with populations of Barbilophozia hatcheri (a liverwort) and Peltigera aphthosa (a lichen) accounted for 94% of the mean cover of the stratum.

The tree stratum (including saplings) has the second highest cover estimate of approximately 50% with a standard deviation of 13.7%. Cover estimates were not obtained by species in the tree stratum but it is estimated that over 90% of the mean cover was accounted for by Engelmann spruce and subalpine fir populations.

In the cover-stratification diagram, the shrub stratum has a vertically defined cover value of 32% made up from the combined cover estimates of "true" shrubs and tree reproduction. By excluding tree reproduction and considering only species maturing in this stratum, it is the most poorly-developed of the four strata, having a mean cover estimate of only 15.8%. Without the influence of Menziesia glabella and Rhododendron albiflorum populations, which accounted for 82% of the shrub cover this stratum would be practically non-existent.

The herb-dwarf shrub stratum has an overall mean cover of 26.4% of which tree seedlings compose only 0.8%. Populations of two dwarf shrubs, Vaccinium scoparium and

Vaccinium membranaceum together with populations of *Lycopodium annotinum* and *Arnica cordifolia* accounted for 58% of the stratum's cover.

The volume of space between the top of the shrub stratum and bottom of the tree canopy is occupied solely by saplings and suppressed individuals of the tree stratum as no subordinate arborescent stratum is present. Thus, it is apparent that the spruce-fir ecosystem of Banff and Jasper National Parks is structurally simple, consisting of only four definable strata; three of them occupy the first six feet of space above the forest floor.

X POPULATION STRUCTURES OF THE MAJOR PLANT SPECIES OF THE SPRUCE-FIR ECOSYSTEM

The previous chapter dealt with some structural attributes of the subalpine spruce-fir ecosystem. Except for a brief mention of dominant plant species in the cover-stratification discussion, no information regarding quantitative significance of species populations within strata was given. The following discussion is devoted to an assessment of the population structures of the major plant species of the four strata.

Tree Stratum

Before describing the population structures of tree species, it was deemed necessary to assess their relative quantitative significance. To do this, a mean Importance Value (Curtis 1959, page 74) was calculated for each of the tree species based on the mean values of basal area, density and frequency, for the 18 stands (Table 15).

mean Importance Value = relative basal area + relative density + relative frequency (relative, expressed as a percentage)

with the sum of the individual Importance Values equalling 300

Engelmann spruce had the highest average Importance Value of 156.1 followed by subalpine fir with a value

Table 15. Mean Relative Basal Area, Density and Frequency Values for Tree Species; Listed in Order of Decreasing Mean Importance Values

Species	Mean Relative Basal Area (%)	Mean Relative Density (%)	Mean Relative Frequency (%)	Mean Importance Value[1]
Engelmann spruce	60.0	46.6	49.5	156.1
Subalpine fir	36.0	50.1	45.7	131.8
Lodgepole pine	1.8	1.2	2.0	5.0
Black spruce	0.9	1.3	1.7	3.9
Whitebark pine	0.8	0.4	0.6	1.8
Alpine larch	0.5	0.4	0.5	1.4

[1]For method of calculation see text, page 97; range is 0-300

of 131.8. None of the remaining four species achieved a mean Importance Value of greater than 5.0 and can, therefore, be regarded as subordinate species of the tree stratum in stands meeting the selection criteria.

Because of the significantly greater importance of spruce and fir and because of their co-dominant position in the sampled subalpine forests, the major portion of the following discussion is given to description and comparison of the populations of these two species.

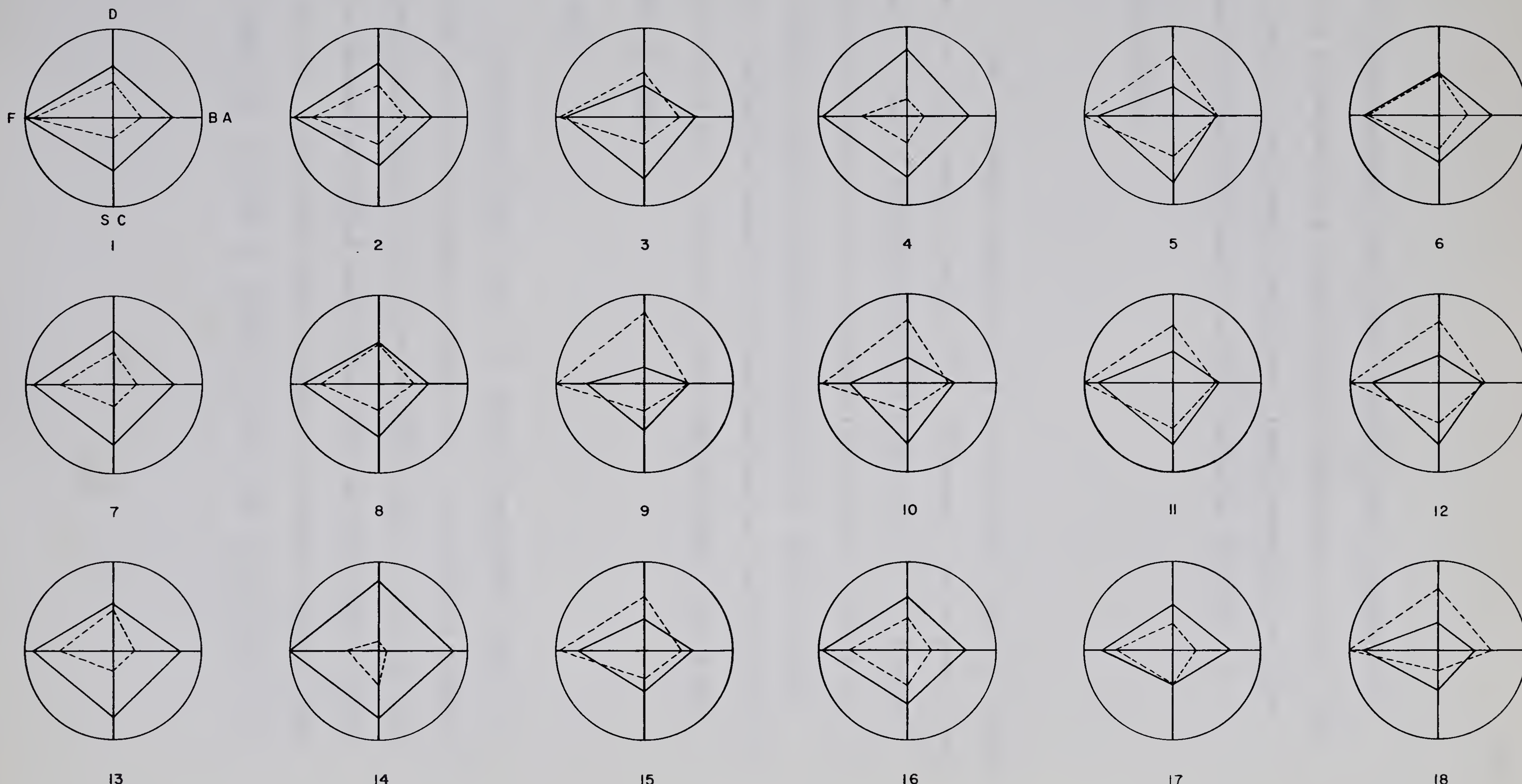
The Dominants

(The following discussion is patterned after Oosting and Reed 1952).

Phytographs (Fig. 7) are used to illustrate the characteristics of the two dominants with respect to density, basal area, size and within-stand distributional pattern (frequency). Density and basal area are expressed as percentages of the respective totals in each stand, so allowing an assessment of the quantitative significance of both species in relation to other members of the stratum. The size-class radius of the phytographs is the maximum diameter class (Table 17, page 107) of each species expressed as a percentage of the diameter of the largest tree found in any stand, an Engelmann spruce measured at 40 inches dbh in Stand 13 (not in a quadrat). Frequency is plotted on the fourth radius of each phytograph. The

Figure 7. Phytographs Comparing Populations of Spruce (——) and Fir (---) in the Eighteen Stands as to Density (D), Basal Area (BA), Size Class (SC), and Frequency (F)

The centre is 0 for each radius and 100% is at the margin. Density and basal area are expressed as percentages of the total in the stand. The size-class radius is the maximum diameter class in the stand expressed as a percentage of the diameter of the largest tree measured.


D
F
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choice of phytographs over more conventional graphical methods is because they permit easy comparison of the two species and at the same time give visual meaning to the importance of the dominants in the various stands.

Population Size

Density

The average density of fir exceeded that of spruce by 5% in the 18 stands (Table 16). However, on a per stand basis spruce had a greater density than fir in 10 stands. The relative density of fir ranged from 12% in Stand 14 to 82% in Stand 9 and was greater than 60% in seven stands (Fig. 7). Relative density of spruce had a range from 18% in Stand 9 to 78% in Stand 14 and was in excess of 60% in only four stands.

Basal Area

The mean basal area of spruce exceeded that of fir by 25% in the 18 stands (Table 16). Fir had a greater basal area than spruce in three stands (No. 5, 12 and 18), but in no stand provided more than 60% of the total basal area (Fig. 7). Relative basal area of spruce ranged from 40% in Stand 18 to 84% in Stand 14 and was over 50% in 15 stands.

Table 16. Density Estimates, Basal Area Estimates and Coefficients of Dispersion for Spruce and Fir

Stand No.	Density (stems per 100 sq m) Spruce	Density (stems per 100 sq m) Fir	Basal Area (sq ft per acre) Spruce	Basal Area (sq ft per acre) Fir	Coefficient of Dispersion[1] Spruce	Coefficient of Dispersion[1] Fir
1	9.4	6.4	107	53	**0.49	**0.49
2	9.6	5.8	93	48	0.81	1.27
3	6.6	7.2	85	59	**0.53	**0.39
4	12.2	3.2	124	34	0.98	1.26
5	5.6	11.2	84	87	**0.48	**0.47
6	7.4	7.2	94	51	*0.70	0.74
7	6.8	4.0	94	38	0.75	0.95
8	7.6	7.2	76	55	††1.29	††2.07
9	3.0	13.4	73	72	*0.54	1.05
10	5.0	12.8	89	79	††1.51	1.11
11	5.8	10.6	87	80	0.76	*0.57
12	5.4	12.0	80	85	†1.50	0.88
13	10.4	9.0	199	61	0.75	††2.90
14	15.2	2.4	164	19	*0.60	††2.00
15	4.8	8.2	90	72	*1.46	*0.64
16	9.8	6.0	143	58	*0.58	1.37
17	6.2	3.6	86	35	**0.44	0.92
18	11.8	26.2	88	130	††2.40	1.00
Total:						
Mean	7.9	8.7	102.8	61.8		
Standard Dev.	3.1	5.4	33.5	25.5		

[1] For method of calculation see text, page 80
Departure from random dispersion towards regular dispersion significant at the 10% level = *, 2% level = **
Departure from random dispersion towards contagious dispersion significant at 10% level = †, significant at 2% level = ††

Tree Diameter

The diameter of the largest spruce was 1.4 times that of the largest fir in all stands except No. 17 in which the diameter of the largest fir was 96% of that of the largest spruce. For the remaining stands the diameters of the largest firs ranged from 34% in Stand 7 to 71% in Stand 11, those of the largest spruce trees.

Diameters of the largest spruce were at least half as large as that of the largest measured tree (size-class radius; Fig. 7, page 100) in all stands except No. 17 and 18. However, only in Stand 11 was the diameter of a fir over 50% of that of the largest tree.

The largest spruce measured in a quadrat was 29.6 inches dbh (Stand 14) while the largest fir measured was only 20.2 inches dbh (Stand 11). Most of the spruce trees were 24 inches dbh or less (Table 17, page 107), whereas, most of the firs were distributed in diameter classes lower than 15 inches.

Tree Height

The average estimated maximum height of spruce was 1.3 times that of fir. In every stand a spruce was the tallest tree measured (Table 10, page 76) whose height was never less than 1.1 times that of the tallest measured fir. The heights of the tallest firs ranged from 53% to

93% of those of the tallest measured spruce trees.

Tree Age

In no stand was the age of the oldest spruce less than 1.2 times that of the oldest fir. The maximum recorded ages of fir trees as a percentage of those of spruce trees, ranged from 35% to 81% in the 18 stands.

Population Pattern

Frequency

Spruce occurred in 87% of the 5m x 5m quadrats, fir in 79%. Spruce had a frequency of 100% in Stands 1 and 14 and in only four stands was its frequency below 80% (Fig. 7, page 100). The frequency of fir was 100% in five stands (No. 5, 9, 11, 12 and 18), and less than 80% in eight stands with the minimum being 35% in Stand 14.

Coefficients of Dispersion

In view of the wide variation in tree frequency, coefficients of dispersion (page 80) were calculated in an attempt to assess the distributional patterns of the two species populations in the various stands. The results are listed in Table 16, page 102.

On a stratum basis, there was a consistently regular distributional patterns of trees (only three stands

departed from regularity; Table 10, page 76). No such consistent pattern existed at the species population level. The patterns of both spruce and fir ranged from highly significant regular distributions to highly significant contagious distributions.

There was a negative correlation ("r" = -0.6217; significant at the 2% level) between the coefficients of dispersion of fir and practical stand age (Table 10, page 76) indicating that the population pattern of fir tends toward regularity with increasing stand age. Based on these data it is hypothesized that the fir populations of younger stands have a contagious distribution, partly because of aggregation of seedlings in favourable microenvironments within the stand and partly because of the asexual reproduction (layering) of fir which causes the formation of clones of young trees. As individuals of the population increase in age and size, they control a volume of space in the stand within which growth and development of other trees is hindered. Thus, as a result of this competition for space, the fir populations have a more regular distribution in older stands.

There was no significant correlation between stand age and the coefficients of dispersion of spruce and based on the limited available data it is impossible to make any generalized hypothesis to account for the extremely

variable distributional pattern of spruce in the sampled subalpine stands.

In summary then, the mean density of fir was greater than that of spruce but spruce had a greater average basal area and a higher frequency than fir, thus explaining its higher Importance Value (Table 15, page 98). Spruce was also older, taller and larger than fir in all stands, further suggesting a relative degree of dominance for spruce over fir. However, from the phytographs (Fig. 7, page 100) it appears that fir was more important than spruce in Stands 5, 9, 10, 11, 12, 15 and 18.

The situation suggests an examination of the population sizes of the two species throughout their ontogenetic development, from seedlings to mature trees, to detect the phytosociological relationship between spruce and fir.

Ontogenetic Development of Spruce and Fir

As seedlings, fir outnumbered spruce 37:1 (Table 17), making it clear that many more fir than spruce become established. Within the transgressive size class, fir continued to outnumber spruce by a ratio of 9:1, although there was good evidence of a relatively high mortality rate of fir seedlings and a relatively high survival rate of spruce seedlings. Fir transgressives showed a reduction in numbers of 83% over the number of fir seedlings, whereas,

Table 17. The Density of Spruce and Fir Seedlings, Transgressives, Saplings and Trees by 3 inch Diameter Classes Expressed as Number of Individuals per 500 sq m

Stand No.		Seedlings under 12 in.	Transgres-sives 12 in.-1 in. tall--dbh	Saplings 1 in.-3 in. dbh	Diameter Classes--inches								
					-6	-9	-12	-15	-18	-21	-24	-27	-30
1	S	-	6	7	-	10	13	9	1	1	1	-	-
	F	375	200	48	23	9	-	-	-	-	-	-	-
2	S	-	13	22	19	11	7	8	2	1	-	-	-
	F	300	31	41	22	6	1	-	-	-	-	-	-
3	S	50	19	5	5	6	4	7	7	2	1	1	-
	F	75	263	50	29	5	2	-	-	-	-	-	-
4	S	-	38	18	27	13	8	3	6	2	-	2	-
	F	450	38	8	9	5	2	-	-	-	-	-	-
5	S	-	-	-	2	2	4	6	6	1	5	1	1
	F	350	225	27	28	16	7	4	1	-	-	-	-
6	S	-	-	11	8	12	9	4	3	1	-	-	-
	F	225	94	16	26	5	1	4	-	-	-	-	-
7	S	-	-	6	9	9	8	5	1	-	-	2	-
	F	125	181	10	15	5	-	-	-	-	-	-	-
8	S	50	69	17	15	7	7	3	3	2	1	-	-
	F	1900	256	47	26	7	3	-	-	-	-	-	-
9	S	-	-	-	3	3	2	3	2	2	-	-	-
	F	475	288	42	39	25	3	-	-	-	-	-	-
10	S	175	19	2	3	8	6	4	2	1	-	1	-
	F	475	425	64	43	18	3	-	-	-	-	-	-
11	S	-	6	1	2	4	4	7	5	2	4	1	-
	F	400	75	52	22	16	9	5	-	1	-	-	-
12	S	-	6	8	11	5	-	2	2	5	1	1	-
	F	1425	119	23	32	11	10	4	3	-	-	-	-
13	S	-	6	2	9	5	5	11	7	7	5	1	1
	F	3100	75	45	33	10	-	-	-	-	-	-	-
14	S	50	56	13	22	23	14	11	3	1	-	1	1
	F	175	6	3	4	4	3	1	-	-	-	-	-
15	S	-	44	9	7	5	5	5	2	-	-	-	-
	F	3800	481	38	26	12	3	-	-	-	-	-	-
16	S	-	6	14	13	13	15	4	-	1	3	-	-
	F	1250	63	17	18	9	2	1	-	-	-	-	-
17	S	150	13	3	8	8	9	6	-	-	-	-	-
	F	875	13	13	12	4	-	2	-	-	-	-	-
18	S	-	31	18	33	16	6	2	2	-	-	-	-
	F	1950	138	115	120	11	-	-	-	-	-	-	-
Total: Mean	S	26.4	18.3	9.0	11.9	9.0	7.2	5.5	3.1	1.7	1.2	0.6	0.2
	F	984.7	165.1	43.3	29.9	10.1	2.9	1.2	0.2	0.1	-	-	-

spruce transgressives showed a reduction of only 31% over the number of spruce seedlings.

At the sapling stage of development, individuals of fir were 4.8 times as numerous as those of spruce. There was a marked decrease in the density of both species over the previous developmental stage; only one-half as many spruce saplings as spruce transgressives and one-fourth as many fir saplings as fir transgressives were found.

In the smallest tree diameter class (3 to 6 inches dbh) fir still outnumbered spruce by a ratio of 2.5:1. Spruce trees in this class were three times as numerous as spruce saplings, while the number of fir trees was only 70% of that of its transgressives.

A density equilibrium point was reached in the 6 to 9 inch diameter class. Here, the ratio of fir to spruce was only 1.1:1 and there were more individuals of spruce than fir in 10 stands. Both species populations showed a decreased density over the previous developmental stage and continued to show such decreases throughout the remaining diameter classes.

In the 9 to 12 inch diameter class there was a reversal in relative proportions of the two species populations. Spruce outnumbered fir by a ratio of 2.5:1 and in only three stands (No. 5, 9, 11) was the density of

fir greater than that of spruce.

Individuals of spruce with diameters between 12 inches and 15 inches were 4.6 times as numerous as individuals of fir in the same diameter range. Firs of this diameter class were present in only seven stands.

In the diameter classes of 15 to 18 inches and 18 to 21 inches, the ratios of spruce to fir increased to 15.5:1 and 17:1 respectively. The remaining classes were occupied exclusively by spruce.

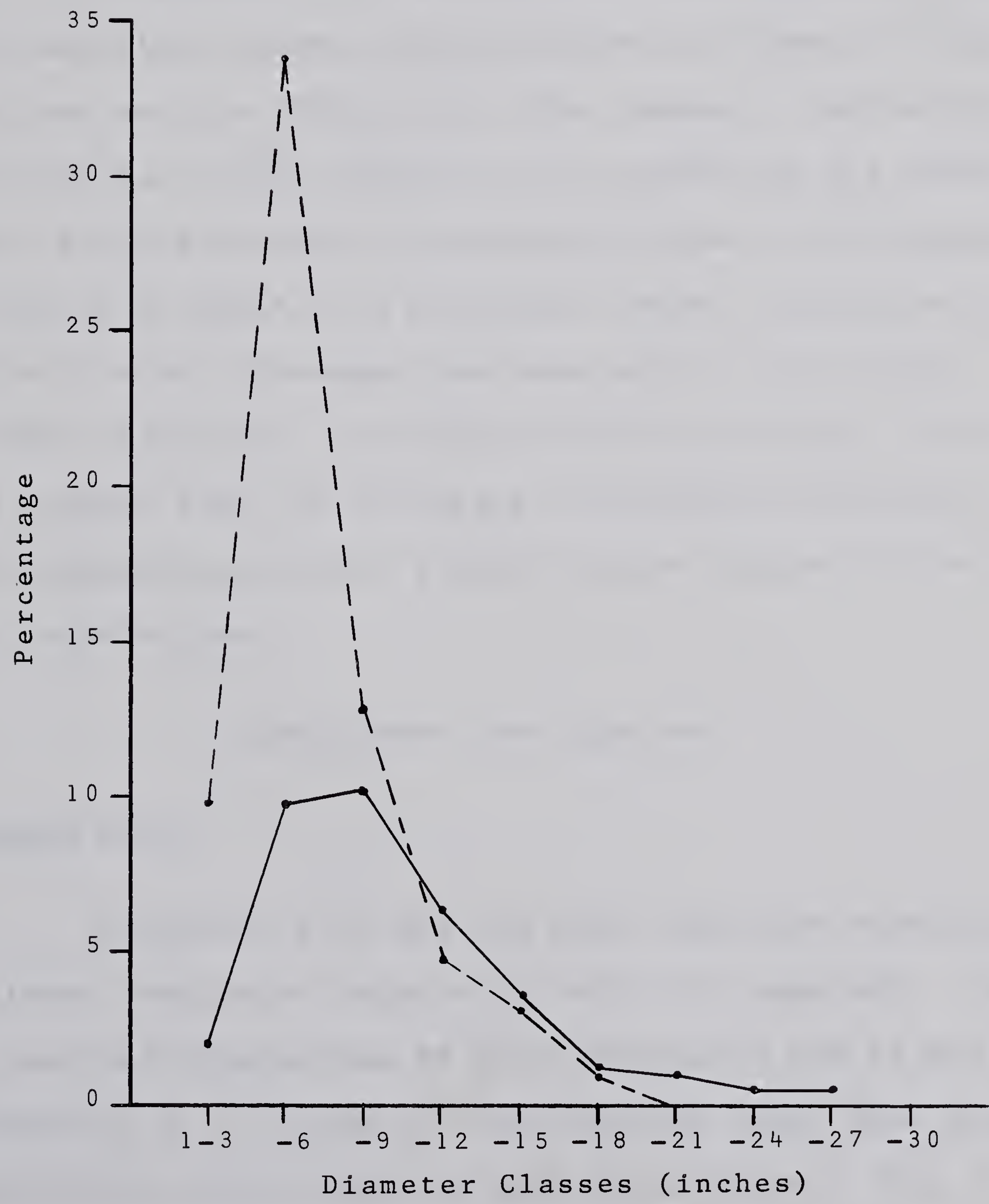
Mortality of Spruce and Fir

In Fig. 8, standing dead spruce and fir as a percentage of the total standing dead trees are plotted against diameter class (seedlings and transgressives are omitted as data were not available). The total standing dead density of fir exceeded that of spruce by 20%.

At the sapling stage of development relatively low numbers of dead spruce and fir were recorded, 9.7% of the total for fir and 2% for spruce. The percentage dead for both spruce and fir populations increased in the 3 to 6 inch diameter class with spruce accounting for 9.7% and fir 33.8% of the total dead.

In the 6 to 9 inch diameter class, fir accounted for 12.8% and spruce 10.2% of the total dead.

Figure 8. Diameter Class Distribution of Standing Dead Spruce (——) and Dead Fir (---) Expressed as a Percentage of the Total Number of Standing Dead Individuals



The percentages of dead individuals of both species decreased steadily throughout the next three diameter classes with spruce accounting for slightly more of the total dead than fir in all classes. Only dead spruce trees were found in the remaining diameter classes and collectively accounted for 3% of the total standing dead.

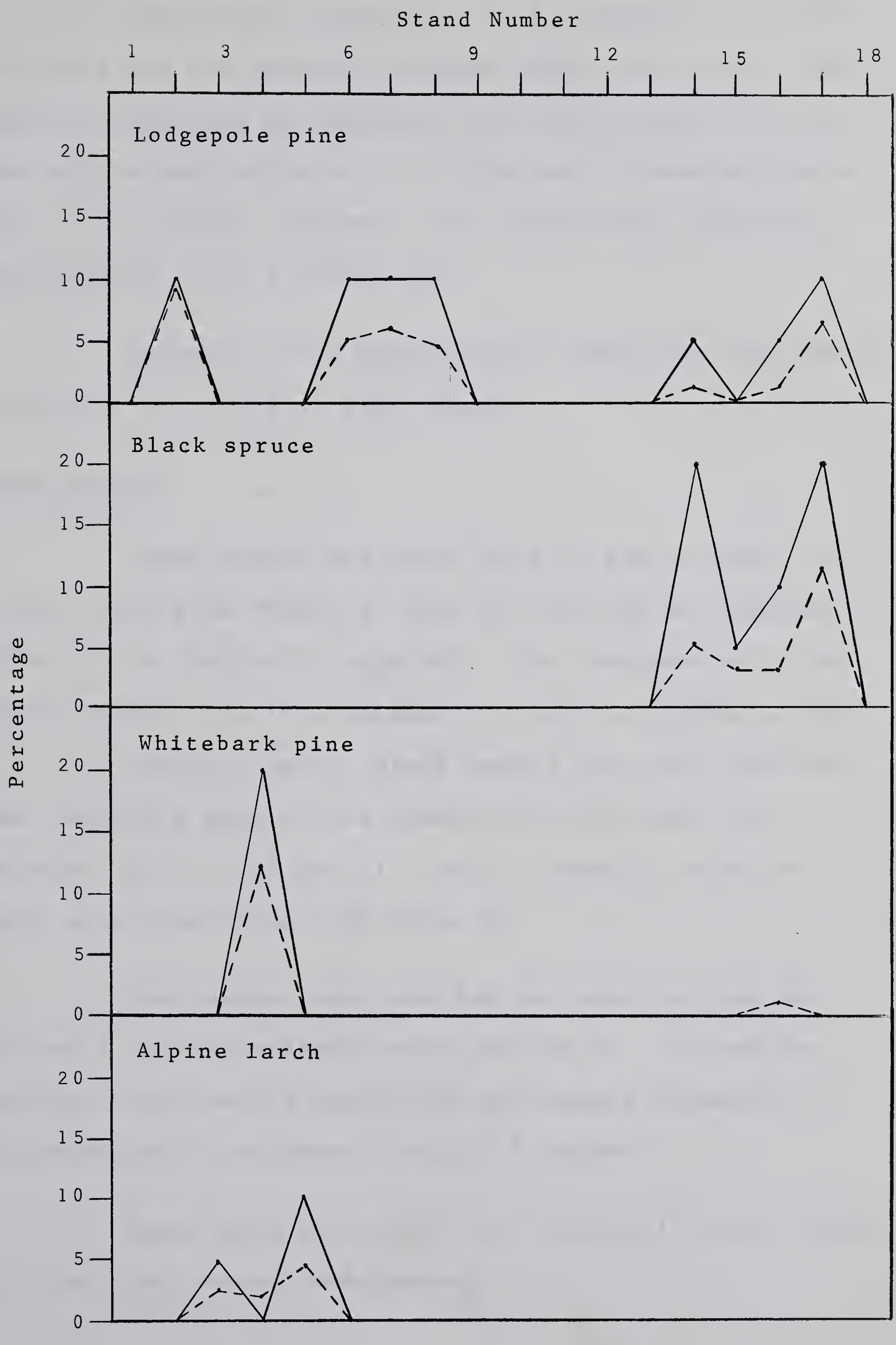
In summary, it is apparent that relatively few spruce seedlings become established but of these, a high proportion survive through all size classes. The reverse is true of fir; large numbers of fir seedlings are established, survive through intermediate stages of development and then as a result of a constant, severe thinning and a relatively short life-span (maximum age of fir is less than that of spruce), succumb in the tree stratum. Thus, it is evident that fir maintains a co-dominant position in the sampled spruce-fir stands only by virtue of its prolific reproduction.

Subordinate Tree Species

Lodgepole Pine

Lodgepole pine was the most important subordinate tree (mean Importance Value = 5; Table 15, page 98). Lodgepole pine had frequencies of 5% in Stands 14 and 16 and 10% in Stands 2, 6, 7, 8 and 17, and relative basal area estimates ranging from 1.8% in Stand 14 to 9.3% in Stand 2 (Fig. 9).

Figure 9. Quadrat Frequencies (——) and Relative Basal Area Estimates (---) for the Four Subordinate Tree Species in the Eighteen Stands



Stand Number
1
3
6
9
12
15
18
Percentage
Lodgepole pine
Black spruce
Whitebark pine
Alpine larch
20
15
10
5
0

The maximum recorded age of lodgepole pine was 230 years and the maximum recorded height was 79 ft. The measured diameters of lodgepole pine were relatively uniform with a mean value of 8.0 inches and a standard deviation of 2.9 inches. However, one exceptional individual was measured at 27.7 inches dbh.

Lodgepole pine reproduction (seedlings and transgressives) was found in four stands.

<u>Black Spruce</u>

Black spruce was found only in the northern part of the study area (Table 4, page 64) and had an Importance Value of 3.9 (Table 15, page 98). The frequency of black spruce ranged from 5% in Stand 15 to 20% in Stands 14 and 17. On a relative basis, black spruce was more important than lodgepole pine in the stands in which they both occurred (No. 14, 16 and 17), with a range of relative basal area from 3% to 7.5% (Fig. 9).

The maximum age recorded for black spruce was 207 years and the maximum height was 54 ft. It was the smallest tree species found with an average diameter of 5.6 inches and a maximum of only 9.1 inches.

Black spruce reproduction was found in all stands in which black spruce was present.

Whitebark Pine

Whitebark pine was quantitatively significant in only two stands (No. 4 and 16; Fig. 9, page 112) and thus had a low Importance Value of 1.8 (Table 15, page 98). The maximum age of whitebark pine was 404 years and the maximum height was 68 ft.

All stages of whitebark pine reproduction were found during the course of the study.

Alpine Larch

Alpine larch was the least important of the tree species with an Importance Value of 1.4 (Table 15). Alpine larch had a maximum frequency of 10% and a maximum relative basal area of 4%, within its restricted southern and high altitudinal distribution (Fig. 9, page 112; Tables: 4, page 64; 5, page 65).

The maximum recorded age of larch was 342 years and the maximum height was 64 ft. Alpine larch reproduction was found in all stands in which larch was present.

Shrub Stratum

Based on the more limited available quantitative information, an assessment of the population structures of shrub species is presented in two steps. Firstly, the species are ranked according to abundance, and secondly

the absolute and relative quantitative significance of the abundant species is given.

Species were ranked according to Abundance Values, synthetic figures representing the quantitative significance of each species.

Abundance Value = $\sqrt{\text{Presence}}$ x mean absolute cover and has a range of 0-1,000

In forming this value, cover was considered to be the most significant quantitative value available and the distribution of species (Presence) was used to modify it. As a species need only occur once in a stand to achieve a Presence Value, the square root was considered to be an adequate modification. The Abundance Value is patterned after the Frequency-Presence Index of Curtis (1959, page 81) and the Prominence Value created and used by Beals (1960). Only species with a cover estimate, and a Presence Value of greater than 20% were assigned Abundance Values. By using 20% Presence as an arbitrary cut-off point, rare or seldom-present species (Oosting 1956, page 73) were omitted. Shrub species are listed in Table 18 in order of decreasing Abundance Values along with Presence Values, mean absolute cover and relative cover (mean cover of a species as a percentage of the stratum cover) values, to show the population structures of species independent of and in relation to other members of the stratum.

Table 18. Presence, Mean Absolute Cover, and Relative Cover Values for Shrub Species, Listed in Order of Decreasing Abundance Values

Species	Presence (%)	Mean Absolute Cover (%)	Relative Cover (%)	Abundance Value[1]
Menziesia glabella	78	10.68	67.60	94.200
Rhododendron albiflorum	61	2.23	14.51	17.923
Ledum groenlandicum	61	1.04	6.58	8.125
Salix drummondiana	89	0.86	5.44	8.110
Juniperus communis	50	0.21	1.33	1.485
Ledum glandulosum	28	0.23	1.47	1.223
Ribes viscosissimum	44	0.18	1.12	1.179
Shepherdia canadensis	33	0.16	0.99	0.906
Betula glandulosa	22	0.04	0.27	0.203
Lonicera involucrata	39	0.01	0.08	0.081
Potentilla fruticosa	28	0.01	0.06	0.053

[1]For method of calculation see text, page 115; range 0-1,000

Menziesia glabella had the highest Abundance Value of any shrub species, with a value of 94.200. It also had the highest mean absolute cover value (10.68%) and accounted for over two-thirds of the total cover of the stratum.

The second most abundant shrub was *Rhododendron albiflorum* with an Abundance Value of only 17.923. For the 18 stands, it attained a mean absolute cover value of 2.23% and accounted for 14.51% of the cover of the stratum.

Ledum groenlandicum and *Salix drummondiana* had similar Abundance Values of 8.125 and 8.110. The relative cover values of *Ledum* and *Salix* were 6.58% and 5.44% respectively.

Based on Abundance Values the other species can be regarded as quantitatively insignificant. Of the remaining seven species, four had Abundance Values between 1 and 1.5 and three had values of 0.2 or less.

In general, then, the structure of the shrub stratum is largely controlled by the populations of four species, *Menziesia glabella*, *Rhododendron albiflorum*, *Ledum groenlandicum* and *Salix drummondiana*, which collectively accounted for 94% of the total shrub cover.

Herb-Dwarf Shrub Stratum

The population structures of herb-dwarf shrub

species were assessed using the same method outlined for the shrub stratum (page 115).

Of the 92 species present in this stratum, 35 had a cover estimate, and a presence value of greater than 20% (arbitrary cut-off point); these were assigned Abundance Values. These species are listed in Table 19, in order of decreasing Abundance Values along with Presence Values, mean absolute cover and relative cover (mean cover of a species as a percentage of the stratum cover) values. Only 13 of the 35 species had Abundance Values which were relatively high.

As for the shrub stratum, the Abundance Values of all species of the herb-dwarf shrub stratum were located in the lower one-tenth of the possible range (0-1,000).

<u>Vaccinium scoparium</u> attained the highest Abundance Value of 89.372. This species also had the highest mean absolute cover of 8.94% and accounted for 34.05% of the stratum's cover, the largest portion accounted for by any species.

The second most abundant species was <u>Vaccinium membranaceum</u> with an Abundance Value of 32.820, a mean cover of 3.58% and a relative cover of 13.64%.

In third position, two species, <u>Lycopodium annotinum</u> and <u>Arnica cordifolia</u> had similar Abundance

Table 19. Presence, Mean Absolute Cover, and Relative Cover Values for Herb and Dwarf Shrub Species, Listed in Order of Decreasing Abundance Values

Species	Presence (%)	Mean Absolute Cover (%)	Relative Cover (%)	Abundance Value[1]
Vaccinium scoparium	100	8.94	34.05	89.372
Vaccinium membranaceum	89	3.58	13.64	32.820
Lycopodium annotinum	83	1.40	5.31	12.735
Arnica cordifolia	94	1.16	4.42	11.275
Phyllodoce glanduliflora	67	1.07	4.07	8.734
Linnaea borealis	50	1.13	4.30	7.975
Elymus innovatus	56	1.00	3.82	7.482
Pyrola secunda	100	0.74	2.81	7.377
Rubus pedatus	28	1.08	4.13	5.707
Phyllodoce empetriformis	56	0.74	2.80	5.491
Cornus canadensis	56	0.68	2.58	5.043
Equisetum scirpoides	56	0.61	2.34	4.573
Cassiope mertensiana	50	0.54	2.07	3.832
Empetrum nigrum	61	0.25	0.94	1.939
Fragaria virginiana	56	0.18	0.67	1.320
Thalictrum occidentale	44	0.18	0.64	1.112
Pedicularis bracteosa	61	0.14	0.51	1.056
Valeriana sitchensis	33	0.17	0.64	0.964
Vaccinium vitis-idaea	39	0.14	0.53	0.867
Moneses uniflora	94	0.07	0.25	0.642
Pyrola virens	83	0.07	0.26	0.612
Arctostaphylos rubra	22	0.11	0.42	0.525
Cassiope tetragona	33	0.07	0.26	0.398
Aquilegia flavescens	33	0.06	0.21	0.323
Trollius albiflorus	44	0.04	0.16	0.280
Parnassia fimbriata	50	0.03	0.11	0.198
Listera cordata	39	0.03	0.11	0.175
Erigeron perigrinus	28	0.03	0.11	0.148
Senecio triangularis	28	0.03	0.11	0.148
Mitella pentandra	22	0.03	0.11	0.132
Stenanthium occidentale	39	0.02	0.08	0.115
Epilobium angustifolium	50	0.01	0.05	0.099
Goodyera repens	33	0.01	0.05	0.081
Achillea millefolium	28	0.01	0.05	0.074

[1]For method of calculation see text, page 115; range 0-1,000

Values of 12.735 and 11.275 respectively. Together they accounted for 9.73% of the stratum's cover.

Abundance Values will be indicated parenthetically after the name of the species in the remainder of the discussion. Phyllodoce glanduliflora (8.734), Linnaea borealis (7.975), Elymus innovatus (7.482) and Pyrola secunda (7.377) formed a species-group based on abundance. The relative contributions to the total cover were similar for all species (range 3.82% to 4.30%) except Pyrola which had a much lower relative cover value (2.81%) and a correspondingly higher Presence of 100%.

A second group of relatively abundant species was composed of Rubus pedatus (5.707), Phyllodoce empetriformis (5.491), Cornus canadensis (5.043), Equisetum scirpoides (4.573) and Cassiope mertensiana (3.832) of which all but Rubus had similar Presence Values, and relative cover values (range 2.07% to 2.80%). Rubus had a low Presence (28%) because of its restricted geographic range (Table 6, page 67); within its area of occurrence, however, Rubus was very abundant, giving it a mean absolute cover of 1.08% and a relative cover value of 4.13%.

The above-mentioned 13 species accounted for 86.34% of the stratum's cover. The remaining 21 species of Table 19 (page 119) are all of low quantitative significance with Abundance Values ranging from 0.074 to 1.939.

Collectively, they accounted for an additional 6.23% of the total cover leaving 8.39% of the herb-dwarf shrub cover to be accounted for by the 57 rare or seldom-present species.

There appeared to be a positive correlation between presence and abundance of the herb-dwarf shrub species, (i.e., species of high presence also had high Abundance Values). There were, however, notable exceptions; for example, Moneses uniflora and Pyrola virens, both had Presence Values of over 80% but made very minor contributions to the structure of the stratum and thus attained Abundance Values of only 0.642 and 0.612 respectively.

This treatment of the population structures of the major species of the vascular strata tends to reinforce the already-presented evidence (page 55) of the floristic simplicity of the subalpine spruce-fir ecosystem. Of the total sample vascular flora of 113 species only two trees, four shrubs and 13 herbs or dwarf shrubs (subtotal of 19) recurred consistently and abundantly in forest stands meeting the selection criteria.

Terrestrial Bryophyte-Lichen Stratum

Because of inaccurate field-determinations of many bryophyte and lichen species, an assessment of the population structures of only the six major species of

of this stratum is presented, using the same method outlined for the shrub stratum (page 115). These species are listed, in order of decreasing Abundance Values, together with Presence Values, mean absolute cover and relative cover values, in Table 20.

Hylocomium splendens, with an Abundance Value of 209.5, was the most abundant member of this stratum followed by *Pleurozium schreberi*, with an Abundance Value of 130.7. *Hylocomium* and *Pleurozium* had mean absolute cover values of 20.95% and 13.07% respectively. Collectively, these two "feather mosses" accounted for 58.85% of the bryophyte-lichen stratum's cover.

Dicranum scoparium and *Ptilium crista-castrensis*, another "feather moss," were ranked third and fourth in importance with Abundance Values of 70.1 and 51.55 and relative cover values of 12.13% and 8.25% respectively.

Barbilophozia hatcheri and *Peltigera aphthosa* were the remaining major species of the bryophyte-lichen stratum with Abundance Values of 47.7 and 36.0 respectively. Together they accounted for 14.48% of the stratum's cover.

The observed floristic simplicity of the vascular strata appears to also be true of the bryophyte-lichen stratum, as the above-mentioned six species populations collectively accounted for 94.37% of the stratum's cover.

Table 20. Presence, Mean Absolute Cover, and Relative Cover Values for Bryophyte and Lichen Species, Listed in Order of Decreasing Abundance Values

Species	Presence (%)	Mean Absolute Cover (%)	Relative Cover (%)	Abundance Value
Hylocomium splendens	100	20.95	36.24	209.5
Pleurozium schreberi	100	13.07	22.61	130.7
Dicranum scoparium	100	7.01	12.13	70.1
Ptilium crista-castrensis	100	5.17	8.91	51.5
Barbilophozia hatcheri	100	4.77	8.25	47.7
Peltigera aphthosa	100	3.60	6.23	36.0

For method of calculation see text, page 115; range 0-1,000

In comparison with the other strata of the sampled subalpine spruce-fir stands, the bryophyte-lichen stratum is not only the best developed (Fig. 6, page 94) but as judged by Abundance Values, contains individual species populations which are much larger than those of either the shrub or herb-dwarf shrub strata.

XI VEGETATION AND ENVIRONMENT

Vegetation Structure and Environment

Thus far, consideration has been given only to the first objective of the study; namely, a synthesis of the general character of the spruce-fir forest. The following chapter will deal with the relation of vegetation to the environment.

Of the various methods of testing the relation between vegetation and environment, simple correlation and multiple regression analyses are considered to be the most appropriate (Greig-Smith 1964, page 125). Both methods have been employed in this study.

The environmental variables used in the correlations are given in Table 21. All variables pertaining to the mineral soil were measured in the lowest horizon of each soil profile (Appendix D, Table D1, page 227), as this was the depth at which the maximum root penetration was observed. Two historical variables pertaining to stand age are given. Age of the oldest tree was used in correlations with vegetation attributes of the tree stratum and practical stand age was used in correlations with attributes of the lower strata. The vegetation variables included in the list are all structural attributes of the tree stratum and were used only in correlations with vegetation attributes of the lower

Table 21. Measured Environmental Variables Used in Simple Correlation and Multiple Regression Analyses

Edaphic variables pertaining to the mineral soil were measured in the lowest horizon of each soil profile; Appendix D, Table D1, page 227.

Physiographic Variables

Latitude (degrees)

Elevation (feet above mean sea level; midpoint of the stand)

Slope angle (degrees; mean value of several spot readings)

Aspect (N = 1, NE and NW = 2, E and W = 3, SE and SW = 4, S = 5)

Light intensity (mean light intensity inside the stand as a percentage of mean light intensity outside the stand)

Edaphic Variables

Thickness of the humus layer (inches)

Fraction of the mineral soil less than 2 mm in size (percentage by weight)

Silt and clay fraction of the mineral soil (percentage by weight of the less than 2 mm size fraction of the mineral soil)

Clay fraction of the mineral soil (percentage by weight of the less than 2 mm size fraction of the mineral soil)

Silt fraction of the mineral soil (percentage by weight of the less than 2 mm size fraction of the mineral soil)

Sand fraction of the mineral soil (percentage by weight of the less than 2 mm size fraction of the mineral soil)

Field capacity of the mineral soil (percentage water content of the oven-dry weight of the less than 2 mm size fraction of the mineral soil)

Permanent wilting percentage of the mineral soil (percentage water content of the oven-dry weight of the less than 2 mm size fraction of the mineral soil)

Table 21. Continued

Available water of the mineral soil (percentage; field capacity of the mineral soil minus permanent wilting percentage of the mineral soil)

Available nitrogen concentration of the humus layer (pounds per acre)

Available phosphorus concentration of the humus layer (pounds per acre)

Available potassium concentration of the humus layer (pounds per acre)

Available nitrogen concentration of the mineral soil (pounds per acre; analysis made on the less than 2 mm size fraction of the mineral soil)

Available phosphorus concentration of the mineral soil (pounds per acre; analysis made on the less than 2 mm size fraction of the mineral soil)

Available potassium concentration of the mineral soil (pounds per acre; analysis made on the less than 2 mm size fraction of the mineral soil)

Hydrogen ion concentration of the humus layer (moles per litre)

Hydrogen ion concentration of the mineral soil (moles per litre; determination made on the less than 2 mm size fraction of the mineral soil)

Historic Variables

Age of oldest tree in the stand (years; age at breast height)

Practical stand age (years; lab method, page 47)

Vegetation Variables

Total tree density of the stand (stems per 100 sq m)

Total basal area of the stand (square feet per acre)

Percentage tree canopy cover (based on tree canopy photographs, lab method, page 45)

Spruce hybrid index (range is 0-400; lab method, page 48)

strata as the structure of the superior stratum was regarded as a part of the environment of the subordinate strata.

Simple Correlation

Using computer techniques, simple correlation coefficients ("r") were made between structural attributes of the four strata and environmental variables (Table 21). The resulting significant coefficients are listed in Table 22 by strata.

These correlation coefficients are measures of the degree of association between the correlated variables and do not infer cause and effect. However, the level of the environmental variable can logically be assumed to be controlling the level of vegetation variable, in the absence of information to the contrary. Such assumptions are usually ecologically justifiable (Greig-Smith 1964, page 125).

Tree Stratum

Total tree density and total basal area were used as representative attributes. Since density and basal area are themselves correlated ("r" = +0.5654), the similarities in their correlations with environmental variables are not surprising. Both attributes showed positive correlations with available phosphorus concentration of the mineral soil, suggesting that tree productivity is in part a function of

Table 22. Correlation Coefficients between Structural Attributes and Environmental Variables

Coefficients shown parenthetically after environmental variable name; significant at 5% level except as marked (*), 10% level. For units of measure of variables refer to Table 21, page 126.

Tree Stratum

<u>Total tree density of the stand</u>

Light intensity (-0.5509)

Available phosphorus concentration of the mineral soil (+0.6866)

Hydrogen ion concentration of the mineral soil (+0.5889)

Available phosphorus concentration of the humus layer *(+0.4476)

<u>Total basal area of the stand</u>

Light intensity (-0.5817)

Available phosphorus concentration of the mineral soil *(+0.4062)

Shrub Stratum

<u>Absolute shrub cover</u>

Total basal area of the stand (-0.6416)

Light intensity *(+0.4209)

Total tree density of the stand *(-0.4173)

Herb-Dwarf Shrub Stratum

<u>Absolute herb-dwarf shrub cover</u>

Available nitrogen concentration of the humus layer (-0.4770)

Table 22. Continued

Bryophyte-Lichen Stratum

Absolute bryophyte-lichen cover

Aspect (-0.8111)

Elevation (-0.4707)

phosphorus concentration of the soil and that an increase in phosphorus will cause an increase in productivity.

Total tree density and total basal area both showed expected negative correlations with light intensity, as light intensity is directly controlled by the structure of the tree stratum; the better developed the tree stratum, the lower the within-stand light intensity.

Total tree density also showed positive correlations with hydrogen ion concentration of the mineral soil and available phosphorus concentration of the humus layer.

Shrub Stratum

Absolute cover was selected as the representative structural attribute of this stratum. The environmental variables significantly correlated with shrub cover were all either direct or indirect attributes of the tree stratum. Absolute shrub cover was positively correlated with light intensity and negatively correlated with total tree density and total basal area. This suggests that the development of the shrub stratum is more a function of the tree canopy development than of physical environmental variables.

Herb-Dwarf Shrub Stratum

Using absolute cover as the structural representative of this stratum, only one significant correlation

with the environment was observed, a negative correlation with available nitrogen concentration of the humus layer. From this it may be hypothesized that sites with nitrogen-rich humus layers have, for some reason, poorly-developed herb-dwarf shrub strata.

Terrestrial Bryophyte-Lichen Stratum

Absolute cover was used as the representative structural attribute of this stratum and showed significant negative correlations with elevation and aspect. This indicates that stands at low elevations or more northerly aspects have better-developed bryophyte-lichen strata.

Multiple Regression Analyses

A serious limitation of simple correlation to accurately show the relation between vegetation and environment is that the mode of calculation ignores simultaneous effects of other variables on one or both of the correlated ones.

In view of this limitation, simple correlation coefficients were not considered completely satisfactory

to show the relation between vegetation and environment because the environment is a network of simultaneously interfacing factors [i.e., "holocoenotic" (Billings 1952)]. In place of simple correlation, stepwise multiple regression was used as it shows the relation between several variables and at the same time takes into account (i.e., corrects for) simultaneous variations in other variables.

The use of multiple regression analyses in vegetation-environment studies has been largely fostered by Coile (1948, 1952) in his studies of soil-site factors and tree growth. Because of the stimulus provided by Coile, combined with the introduction of electronic computing facilities, many researchers have used this technique in vegetation-environment studies.

There are two major advantages of multiple regression. Firstly, it allows a quantitative prediction of vegetation attributes from measured environmental variables, and secondly, it selects out what are probably the most operative environmental factors from all the measured ones (Scott and Billings 1964).

The stepwise multiple regression analyses were done using the Multiple Regression Program No. G2011, Department of Computing Science, University of Alberta, written in Fortran IV for the I.B.M. 7040 digital computer and explained in Publication No. 1 of the Department of Computing Science (Smillie 1965).

Because the regression program limited the number of independent variables (including transformations, see below) to 49, it was necessary to select environmental variables which would be allowed to participate in the regressions. This selection was made from the measured environmental variables listed in Table 21 (page 126) as indicated in the following paragraph.

Using computer techniques, a matrix of simple correlation coefficients ("r") was obtained to estimate the degree of association between the environmental variables. From this matrix it was found possible to separate the initial variables into groups within which all participants were highly correlated (significant positive and negative correlations at the 2% level). These groups are given in Table 23. One variable representing each group was selected to participate as an independent variable in the regression analyses (underlined variables in the table). The variables selected were not present in any other correlation group.

As the purpose of the regression analyses was to

Table 23. Groups of Correlated Environmental Variables; Underlined Variables Selected as Independent Variables for Regression Analyses

Correlation coefficients "r" between underlined variable and group members shown parenthetically after variable name; all coefficients significant at 2% level; "r" = 0.5425. For units of measure refer to Table 21, page 126.

1. <u>Slope angle</u>

   Clay fraction of the mineral soil (-0.5449)

   Permanent wilting percentage of the mineral soil (+0.5644)

2. <u>Silt and clay fraction of the mineral soil</u>

   Clay fraction of the mineral soil (+0.6545)

   Silt fraction of the mineral soil (+0.8329)

   Sand fraction of the mineral soil (-1.0000)

   Fraction of the mineral soil less than 2 mm in size (+0.6123)

3. <u>Available phosphorus concentration of the mineral soil</u>

   Light intensity (-0.5492)

   Total tree density of the stand (+0.6866)

4. <u>Thickness of the humus layer</u>

   Permanent wilting percentage of the mineral soil (+0.5488)

5. <u>Hydrogen ion concentration of the mineral soil</u>

   Available phosphorus concentration of the humus layer (+0.7496)

   Light intensity (-0.6185)

   Total tree density of the stand (+0.5890)

Table 23. Continued

6. <u>Hydrogen ion concentration of the humus layer</u>

   Available potassium concentration of the humus layer (-0.6719)

   Available nitrogen concentration of the humus layer (-0.5769)

7. <u>Available water of the mineral soil</u>

   Field capacity of the mineral soil (+0.8841)

   Silt fraction of the mineral soil (+0.5844)

   Permanent wilting percentage of the mineral soil (+0.5427)

   Available nitrogen concentration of the mineral soil (+0.5812)

8. <u>Elevation</u>

   Latitude (-0.5501)

   Spruce hybrid index (+0.5904)

9. *<u>Age of the oldest tree</u>

   †<u>Practical stand age</u> (+0.7624)

   Spruce hybrid index (+0.6125)

10. †<u>Total basal area of the stand</u>

    Light intensity (-0.5817)

    Total tree density of the stand (+0.5654)

    Percentage tree canopy cover (+0.5788)

11. <u>Aspect</u>

12. <u>Available potassium concentration of the mineral soil</u>

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*Used only in regression analyses in which the dependent variable was an attribute of the tree stratum

†Used only in regression analyses in which the dependent variable was an attribute of either the shrub, herb-dwarf shrub or bryophyte-lichen strata

detect relationships between vegetation and environment and since these relationships are seldom linear, new variables were generated from the selected ones by the use of non-linear transformations. With the exception of slope angle, three new variables of the form X^2, X^3 and $\log_{10}X$ were generated from each initial variable. One new variable was generated from the slope-angle: the cosine slope angle. The initial variables, together with their transformations, (Table 24) were used as independent variables in the regression analyses. It is obvious that the transformations are independent in name only, but this is of little consequence since the mode of calculation of a multiple regression takes into account any correlation between the independent variables (Greig-Smith 1964, page 127).

Using continuous vegetation variables (present in every stand) as Y and environmental variables (including transformations) as X, it was desired to fit a regression function of the form:

$$Y = c + b_1X_1 + b_2X_2 + b_3X_3 \; ......b_nX_n$$

where, Y = the dependent variable

c = the equation constant

b = the regression coefficient

X = the independent variable

As perfect fit to a set of N observations would be obtained with N - 1 terms in X, the maximum number of

Table 24. Independent Variables Used in Regression Analyses

Edaphic variables pertaining to the mineral soil were measured in the lowest horizon of each soil profile; (Appendix D, Table D1, page 227).

Physiographic Variables

Variable No.	Description of Variable
X_1	Elevation (feet above mean sea level; midpoint of the stand)
X_2	$(X_1)^2$
X_3	$(X_1)^3$
X_4	$\log_{10} X_1$
X_5	Aspect (N = 1, NE and NW = 2, E and W = 3, SE and SW = 4, S = 5)
X_6	$(X_5)^2$
X_7	$(X_5)^3$
X_8	$\log_{10} X_5$
X_9	Slope angle (degrees; mean value of several spot readings)
X_{10}	Cosine X_9

Edaphic Variables

Variable No.	Description of Variable
X_{11}	Silt and clay fraction of the mineral soil (percentage by weight of the less than 2 mm size fraction of the mineral soil)
X_{12}	$(X_{11})^2$
X_{13}	$(X_{11})^3$

Table 24. Continued

<u>Edaphic Variables</u> (Continued)

Variable No.	Description of Variable
X_{14}	$\log_{10} X_{11}$
X_{15}	Available water of the mineral soil (percentage; field capacity of mineral soil minus permanent wilting percentage of the mineral soil; lab method, page 52)
X_{16}	$(X_{15})^2$
X_{17}	$(X_{15})^3$
X_{18}	$\log_{10} X_{15}$
X_{19}	Thickness of the humus layer (inches)
X_{20}	$(X_{19})^2$
X_{21}	$(X_{19})^3$
X_{22}	$\log_{10} X_{19}$
X_{23}	Hydrogen ion concentration of the humus layer (moles per litre)
X_{24}	$(X_{23})^2$
X_{25}	$(X_{23})^3$
X_{26}	$\log_{10} X_{23}$
X_{27}	Available potassium concentration of the mineral soil (pounds per acre; analysis made on the less than 2 mm size fraction of the mineral soil)
X_{28}	$(X_{27})^2$
X_{29}	$(X_{27})^3$
X_{30}	$\log_{10} X_{27}$
X_{31}	Available phosphorus concentration of the mineral soil (pounds per acre; analysis made on the less than 2 mm size fraction of the mineral soil)

Table 24. Continued

Edaphic Variables (Continued)

Variable No.	Description of Variable
X_{32}	$(X_{31})^2$
X_{33}	$(X_{31})^3$
X_{34}	$\log_{10} X_{31}$
X_{35}	Hydrogen ion concentration of the mineral soil (moles per litre; determination made on the less than 2 mm size fraction of the mineral soil)
X_{36}	$(X_{35})^2$
X_{37}	$(X_{35})^3$
X_{38}	$\log_{10} X_{35}$

Historic Variables

Variable No.	Description of Variable
$*X_{39}$	Age of oldest tree in stand (years; age at breast height)
$*X_{40}$	$(X_{39})^2$
$*X_{41}$	$(X_{39})^3$
$*X_{42}$	$\log_{10} X_{39}$
$\dagger X_{43}$	Practical stand age (years; lab method, page 47)
$\dagger X_{44}$	$(X_{43})^2$
$\dagger X_{45}$	$(X_{43})^3$
$\dagger X_{46}$	$\log_{10} X_{43}$

Footnotes at the end of the table on page 141

Table 24. Continued

Vegetation Variables

Variable No.	Description of Variable
†X_{47}	Total basal area of the stand (square feet per acre)
†X_{48}	$(X_{47})^2$
†X_{49}	$(X_{47})^3$
†X_{50}	$\log_{10}X_{47}$

*Used only in regression analyses in which the dependent variable was an attribute of the tree stratum
†Used only in regression analyses in which the dependent variable was an attribute of either the shrub, herb-dwarf shrub or bryophyte-lichen strata

terms in the equations was arbitrarily set at six, a point well below N (N = 18 stands). This arbitrary cut-off level was used, as no completely satisfactory method for termination of a regression equation in which the number of variables greatly exceeds the number of observations is available (Dr. K. W. Smillie, Department of Computing Science, University of Alberta; personal communication). If, however, an optimal fit was observed before the six-term limit was reached, as indicated by the failure of any additional terms to significantly reduce the residual variation, the regression was terminated at this point.

The regression analyses results can be interpreted by assuming, subject to experimental proof or refutation, that the appearance of an environmental variable in the equation indicates a cause-and-effect relationship between it and the dependent variable.

It must be emphasized, however, that a variable appearing as a term in an equation may not be the actual causal agent; it is the selected representative of a correlation group containing related environmental factors, both measured (Table 23, page 135) and unmeasured, any one or more of which may be the true causal agent. For example, where total basal area of the stand appears as an independent variable in an equation, the controlling factor may actually be light intensity, or where elevation appears,

the ultimate factors may be such things as temperature or snow depth which vary with elevation.

Stepwise multiple regression analyses were done using the following five selected structural attributes of the four strata of the spruce-fir stands as dependent variables.

$Y_{(1)}$ Total tree density

$Y_{(2)}$ Total basal area

$Y_{(3)}$ Absolute cover of the shrub stratum

$Y_{(4)}$ Absolute cover of the herb-dwarf stratum

$Y_{(5)}$ Absolute cover of the bryophyte-lichen stratum

The resulting equations are listed in tabular form in Tables 25 and 26. The variables of an equation are listed in the stepwise order in which they were introduced. The first variable of an equation is the one that accounted for the greatest amount of the variation of the dependent variable amongst all the independent ones (i.e., had the highest simple correlation coefficient). The second variable introduced, accounted for the greatest amount of the residual variation of the dependent variable after the effects of the first one had been removed, (i.e., the variation of the first variable was held constant), and so on. In some of the equations, a variable introduced late in the regression

accounted for a higher percentage of the variation of the dependent variable than did previously introduced variables. It would seem that this is because once the "masking" effects of the other independent variables were removed a highly significant relation between the dependent variable and the independent one in question became apparent. The total variation of the dependent variable accounted for by its equation is given at the bottom of the tables.

Tree Stratum

Of the 42 independent variables participating in the regressions (Table 24, page 138) those pertaining to the humus layer deserve special mention. The humus layer is obviously not entirely independent of the tree stratum, as trees are responsible for the development of the humus layer to a large extent. However, it was felt that at early stages in the ontogenetic development of the trees, the humus layer very greatly affected them and thus indirectly aided in controlling the structure of the tree stratum. For this reason variables of the humus layer were allowed to take part in the regressions.

Total Tree Density (Y_1)

The equation consisted entirely of edaphic variables and accounted for 95.74% of the variation of the dependent variable. The most important variable in the

Table 25. Multiple Regression Equations for Total Tree Density and Total Basal Area

Total Tree Density (Y_1) (stems per 100 sq m)			Total Basal Area (Y_2) (sq ft per acre)		
Equation Constant = -23.3390			Equation Constant = 295.238		
R. C.[1]	Var.[2]	V. A.[3]	R. C.[1]	Var.[2]	V. A.[3]
0.002015	X_{33}(e)	84.94	2.58744	X_7 (p)	21.23
-0.029094	X_{27}(e)	3.00	0.056513	X_{32}(e)	21.32
-0.028459	X_{32}(e)	3.48	-0.000295	X_3 (p)	17.33
0.004816	X_{36}(e)	1.06	0.206527	X_{22}(e)	8.65
8.55329	X_{14}(e)	1.56	8.64076	X_{34}(e)	7.87
13.9976	X_{30}(e)	1.70	-254.429	X_8 (p)	4.29
Total V. A.[4] = 95.74			Total V. A.[4] = 80.69		

[1]Regression coefficients
[2]Environmental variable number; refer to Table 24, page 138 for names; lower case letters after variable numbers refer to "e"--edaphic, "p"--physiographic
[3]Percentage variation of the dependent variable accounted for by each term of the equation
[4]Total percentage variation of the dependent variable accounted for by the equation

equation was (available phosphorus concentration of the mineral soil)^3, which accounted for 84.94% of the variation of the dependent variable. The remaining variables were available potassium concentration of the mineral soil, (available phosphorus concentration of the mineral soil)^2, $\log_{10}$percentage silt + clay and $\log_{10}$available potassium concentration of the mineral soil.

Total Basal Area (Y_2)

The basal area equation contained three physiographic and three edaphic variables and accounted for 80.69% of the variation of the dependent variable. The first two terms of the equation were (aspect)^3 and available phosphorus concentration of the mineral soil which together accounted for 42.56% of the variation. The third and fourth terms were (elevation)^3 and thickness of the humus layer. The remaining two terms were $\log_{10}$available phosphorus concentration of the mineral soil and $\log_{10}$aspect.

Although density and basal area are not independent of each other, their regression equations are very different. In terms of the total variation accounted for, the density equation is the more satisfactory. Total tree density appears to be largely a function of available nutrients of the soil with other edaphic factors playing minor roles. Total basal area appears to be a function of both edaphic conditions and physiography. The appearance

of physiographic variables as terms in the equation is almost certainly representative of unmeasured factors which vary with physiography; for example, length of growing season, which varies with elevation, and amount of insolation, which varies with aspect.

Lower Strata

In the regression analyses of the structure of the lower strata, vegetation variables; namely, total basal area and its various transformations were allowed to participate as independent variables and practical stand age was substituted for the age of the oldest tree. Only one regression equation was written for each stratum using absolute cover values as dependent variables. The resulting equations are presented in Table 26.

Absolute Cover of the Shrub Stratum (Y_3)

The equation contained two vegetation variables and four edaphic variables and accounted for 89.13% of the variation of the dependent variable. Log_{10}total basal area and total basal area were the first two variables in the equation. The remaining terms all pertained to hydrogen ion concentration of the humus layer and mineral soil.

Development of the shrub stratum seems to be controlled by the development of the tree stratum, both directly (basal area terms) and indirectly (terms pertaining to

Table 26. Multiple Regression Equations for Absolute Shrub Cover, Absolute Herb-Dwarf Shrub Cover and Absolute Bryophyte-Lichen Cover

Absolute Shrub Cover (Y_{13})			Absolute Herb-Dwarf Shrub Cover (Y_{14})			Absolute Bryophyte-Lichen Cover (Y_{15})		
Equation Constant = 1473.75			Equation Constant = 33.2303			Equation Constant = -2525.25		
R. C.[1]	Var.[2]	V. A.[3]	R. C.[1]	Var.[2]	V. A.[3]	R. C.[1]	Var.[2]	V. A.[3]
-748.737	X_{50}(v)	42.46	0.082029	X_{21}(e)	17.25	-36.6183	X_5 (p)	65.78
1.27536	X_{47}(v)	15.91	6.86068	X_{24}(e)	11.00	-0.000984	X_3 (p)	10.49
0.942830	X_{23}(e)	6.95	0.0000696	X_{13}(e)	9.69	1630.15	X_4 (p)	6.50
0.024478	X_{36}(e)	5.61	-0.0000013	X_{45}(h)	11.24	0.000123	X_{25}(e)	1.00
-16.3949	X_{38}(e)	14.11	-75.2115	X_{22}(e)	15.33	-0.900248	X_{23}(e)	2.93
-0.0000417	X_{26}(e)	4.08	0.973251	X_9 (p)	9.90	0.139433	X_{27}(e)	4.02
Total V. A.[4] = 89.13			Total V. A.[4] = 74.42			Total V. A.[4] = 90.72		

[1] Regression coefficients

[2] Environmental variable number; refer to Table 24, page 138 for names; lower case letters after variable numbers refer to "v"--vegetation, "e"--edaphic, "h"--historic, "p"--physiographic

[3] Percentage variation of the dependent variable accounted for by each term of the equation

[4] Total percentage variation of the dependent variable accounted for by the equation

variables of the humus layer). The appearance of basal area as a term in the equation can probably best be interpreted as relating to light intensity as these two variables were strongly correlated ("r" = -0.5817).

Absolute Cover of the Herb-Dwarf Shrub Stratum (Y_4)

The equation contained four edaphic variables, one historic variable and one physiographic variable, and accounted for 74.42% of the variation of the dependent variable. The first two variables entered into the equation were (thickness of the humus layer)^3 and (hydrogen ion concentration of the humus layer)^2. A textural variable of the mineral soil, (silt + clay)^3, was in third position. (Practical stand age)^3, $\log_{10}$thickness of the humus layer and slope angle were the remaining terms of the equation.

The structure of the herb-dwarf shrub stratum seems to be indirectly controlled by the development of the tree stratum as variables pertaining to the humus layer are most influential in its equation. Physical soil properties, stand age and physiography are of less importance.

Absolute Cover of the Bryophyte-Lichen Stratum (Y_5)

The equation for bryophyte-lichen cover included three physiographic and three edaphic variables and accounted for 90.72% of the variation of the dependent variable. The first three terms of the equation were aspect,

$(\text{elevation})^3$ and $\log_{10}$elevation. These terms collectively accounted for 82.77% of the variation. The remaining terms, two pertaining to hydrogen ion concentration of the mineral soil and the other being available potassium concentration of the mineral soil, accounted for an additional 7.95% of the variation of the dependent variable.

In contrast to the shrub and herb-dwarf shrub strata, the development of the terrestrial bryophyte-lichen stratum appears to be independent of environment created by the tree stratum. Environmental variables manifested through elevation and aspect are of prime importance. Soil acidity and nutrient concentration of the soil seem to control the development of the stratum to a lesser extent.

Species Population Sizes and Environment

The population structures of species were assessed on a purely vegetational basis in Chapter X. Inasmuch as species populations are simultaneously affected by all parts of the environment, it was considered desirable to obtain estimates of the sizes of species populations in relation to their operative environments. To achieve this end, the same multiple regression technique outlined for the structural attributes was applied, using quantitative species information as the dependent variables.

Regression equations were written for eight major

species of the four strata. Two regressions were made for both spruce and fir using their respective density and basal area estimates as dependent variables (Table 27, page 153).

One shrub species and four high presence herb-dwarf shrub species were represented by regression equations using Prominence Values (Beals 1960; values are given in Tables: 6, page 67; 8, page 70) as the dependent variables (Tables: 28, page 158; 29, page 160).

$$\text{Prominence Value} = \sqrt{\text{frequency}} \times \text{absolute cover} + 1$$

where frequency is expressed as a proportion and the value has a range of 1-101

In forming these values, cover was regarded as the most important attribute of any species and was therefore given more weight. Species with the same cover values would, however, have different Prominence Values depending on their distribution (frequency) within the stand. Every species that was present in a stand was assigned a value of one, regardless of whether or not it had a cover value or a frequency value.

Regression equations were written for the two most abundant bryophyte species, using absolute cover as the dependent variable (Table 30, page 165).

Tree Stratum

Density of Engelmann Spruce (Y_6)

The equation accounted for 77.48% of the variation of Engelmann spruce density and was composed entirely of edaphic variables. The first two terms of the equation were $\log_{10}$hydrogen ion concentration of the mineral soil and (available phosphorus concentration of the mineral soil)^3, which collectively accounted for 48.39% of the variation of the dependent variable. The third and fourth terms of the equation were (hydrogen ion concentration of the humus layer)^3 and (hydrogen ion concentration of the humus layer)^2. The remaining two terms were hydrogen ion concentration of the mineral soil and available potassium concentration of the mineral soil.

Basal Area of Engelmann Spruce (Y_7)

The equation for basal area of spruce took a very different form than the density equation. It included three physiographic variables and three edaphic variables, and accounted for 84.76% of the variation of the dependent variable. The first three terms of the equation were (aspect)^3, $\log_{10}$elevation and (thickness of the humus layer)^3, which collectively accounted for 68.29% of the variation. The other terms were (elevation)^2, $\log_{10}$hydrogen ion concentration of the mineral soil and (available water of the mineral

Table 27. Multiple Regression Equations for Density and Basal Area of Engelmann Spruce and Subalpine Fir

Density of Engelmann Spruce (Y_6) (stems per 100 sq m)			Basal Area of Engelmann Spruce (Y_7) (sq ft per acre)		
Equation Constant = 4.30199			Equation Constant = 7824.95		
R. C.[1]	Var.[2]	V. A.[3]	R. C.[1]	Var.[2]	V. A.[3]
-3.31511	X_{38}(e)	21.97	1.06841	X_7 (p)	34.70
0.000271	X_{33}(e)	26.42	-4837.05	X_4 (p)	26.61
0.000028	X_{25}(e)	7.86	-0.210534	X_{21}(e)	6.98
-0.002161	X_{24}(e)	7.30	0.242445	X_2 (p)	9.46
0.186288	X_{36}(e)	5.08	-10.3989	X_{38}(e)	2.60
0.019851	X_{27}(e)	8.85	-0.001426	X_{16}(e)	4.41
	Total V. A.[4] = 77.48			Total V. A.[4] = 84.76	

Density of Subalpine Fir (Y_8) (stems per 100 sq m)			Basal Area of Subalpine Fir (Y_9) (sq ft per acre)		
Equation Constant = -42.1036			Equation Constant = 19.4002		
R. C.[1]	Var.[2]	V. A.[3]	R. C.[1]	Var.[2]	V. A.[3]
0.000935	X_{33}(e)	68.45	1.87136	X_{35}(e)	54.79
1.43713	X_{38}(e)	10.55	6.61913	X_{34}(e)	12.75
16.4037	X_{42}(h)	4.29	0.007502	X_{12}(e)	9.86
-11.3757	X_8 (p)	3.13	1.11912	X_9 (p)	2.72
7.32444	X_{14}(e)	3.89	-4.51866	X_5 (p)	1.77
-0.00000031	X_{29}(e)	2.17	-	-	-
	Total V. A.[4] = 92.48			Total V. A.[4] = 81.90	

[1] Regression coefficients
[2] Environmental variable number; refer to Table 24, page 138 for names; lower case letters after variable numbers refer to "e"--edaphic, "p"--physiographic, "h"--historic
[3] Percentage variation of the dependent variable accounted for by each term of the equation
[4] Total percentage variation of the dependent variable accounted for by the equation

soil)^3. Of these three, (elevation)^2 accounted for the largest portion of the remaining variation.

Density of Subalpine Fir (Y_8)

The equation for density of fir contained four edaphic variables, one physiographic variable and one historic variable; it accounted for 92.48% of the variation of the dependent variable. The most important variables in the equation, in terms of variation accounted for, were (available phosphorus concentration of the mineral soil)^3 and $\log_{10}$hydrogen ion concentration of the mineral soil, which collectively accounted for 79.00% of the variation. The remaining terms were $\log_{10}$age of the oldest tree, $\log_{10}$ aspect, $\log_{10}$silt + clay and (available potassium concentration of the mineral soil)^3.

Basal Area of Subalpine Fir (Y_9)

The equation consisted of only five terms, as the introduction of additional variables failed to significantly reduce the residual variation of the dependent variable. The equation included three edaphic variables and two physiographic variables, and accounted for 81.90% of the variation of the dependent variable. The edaphic variables were hydrogen ion concentration of the mineral soil, $\log_{10}$available phosphorus concentration of the mineral soil and (silt + clay)^2, which collectively accounted for 77.40% of the

variation. The physiographic variables, slope angle and aspect, occurred as the fourth and fifth terms of the equation.

The density equations for spruce and fir both included variables pertaining to available phosphorus concentration of the mineral soil, hydrogen ion concentration of the mineral soil and available potassium concentration of the mineral soil. The basal area equations for spruce and fir both included variables pertaining to hydrogen ion concentration of the mineral soil and aspect. These similarities in the environmental dependencies of the two species suggest an overlap of their ecological amplitudes and may in part account for their co-existence in the sampled subalpine forests.

The equations for density and basal area of spruce contained variables which were not present in the parallel equations written for fir. Similarly, the density and basal area equations for fir included variables not present in the matching spruce equations. The equations for spruce and fir also differed in the form and arrangement of the variables common to both species.

Based on the observed differences in the environmental requirements of the two species, within a similar area of distribution, it is hypothesized that spruce and fir are dependent on and limited by different combinations of environmental factors. That is to say, each species

has its own niche within the subalpine forests meeting the selection criteria and thus they can co-exist in a state of equilibrium.

Based on the different niche requirements and the variable importance of spruce and fir in the sampled stands (Fig. 7, page 100) it is also hypothesized that certain habitats favour the growth and development of either spruce or fir; therefore, spruce and fir will reach their population maxima on different sites. The apparent habitat preferences of the two species suggest that the observed population sizes of spruce and fir in sampled subalpine stands will remain in the same relative proportions, barring catastrophic environmental disturbances which would change the operative environment of the area. This hypothesis is in part supported by field observations. In stands where either spruce or fir was the most important tree, there was no evidence of large numbers of standing or fallen dead of the lesser species to suggest a slow change in the relative dominance of the two species.

However, the physical environment cannot alone determine the population sizes of spruce and fir. The actual cause of the varying population sizes of the two species is probably a result of the combined effects of the operative environment and the phytosociological relationship of spruce and fir, described in Chapter X.

Shrub Stratum

Menziesia glabella (Y_{10})

The equation included three edaphic variables, two physiographic variables and one vegetation variable; it accounted for 85.10% of the variation of the dependent variable. The three most important variables in the equation, in terms of the amount of variation accounted for, were $\log_{10}$available phosphorus concentration of the mineral soil, $\log_{10}$elevation and $\log_{10}$total basal area, which collectively accounted for 68.69% of the variation. The remaining variables of the equation were $(\text{elevation})^2$, $(\text{thickness of the humus layer})^3$ and thickness of the humus layer.

The population size of *Menziesia glabella* appears to be largely a function of available phosphorus concentration of the mineral soil and environmental variables manifested through elevation; for example, length of growing season or temperature.

In comparison with the development of the stratum as a whole, *Menziesia* seems to be much less dependent on the environment created by the tree stratum.

Herb-Dwarf Shrub Stratum

Vaccinium scoparium (Y_{11})

The equation consisted of four edaphic variables,

Table 28. Multiple Regression Equation for <u>Menziesia glabella</u> (Y_{10})

Prominence Value[1] is used as the dependent variable.

Equation Constant = 6001.96

R. C.[2]	Var.[3]	V. A.[4]
-45.9101	X_{30} (e)	27.65
-3625.39	X_4 (p)	18.76
-81.2709	X_{50} (v)	22.27
0.195251	X_2 (p)	5.60
-0.140568	X_{21} (e)	3.77
48.5926	X_{22} (e)	7.04

Total V. A.[5] = 85.10

[1] Prominence Value = $\sqrt{\text{frequency}}$ x absolute cover + 1
[2] Regression coefficients
[3] Environmental variable number; refer to Table 24, page 138 for names; lower case letters after variable numbers refer to "e"--edaphic, "p"--physiographic, "v"--vegetation
[4] Percentage variation of the dependent variable accounted for by each term of the equation
[5] Total percentage variation of the dependent variable accounted for by the equation

two physiographic variables and accounted for 84.29% of the variation of the dependent variable. The first three terms in the equation were $(\text{elevation})^2$, $(\text{thickness of the humus layer})^3$ and $(\text{hydrogen ion concentration of the mineral soil})^2$, which accounted for 59.27% of the variation. The remaining terms were hydrogen ion concentration of the humus layer, $(\text{elevation})^3$ and $(\text{hydrogen ion concentration of the mineral soil})^3$.

Pyrola secunda (Y_{12})

The equation included only edaphic variables and accounted for 89.04% of the variation of the dependent variable. The first two terms were $(\text{silt + clay})^3$ and $(\text{silt + clay})^2$, which accounted for 53.52% of the variation. The remaining terms were $(\text{hydrogen ion concentration of the mineral soil})^3$, $(\text{available phosphorus concentration of the mineral soil})^2$, $\log_{10}$available potassium concentration of the mineral soil and available potassium concentration of the mineral soil.

Arnica cordifolia (Y_{13})

Three edaphic variables, two physiographic variables and one vegetation variable were included in this equation, which accounted for 80.96% of the variation of the dependent variable. The most important variable was $(\text{total basal area})^3$, which accounted for 46.59% of the

Table 29. Multiple Regression Equations for Four High Presence Herb-Dwarf Shrub Species

Prominence Values[1] are used as the dependent variables.

<u>Vaccinium</u> <u>scoparium</u> (Y_{11})

R. C.[2]	Var.[3]	V. A.[4]
	Equation Constant = 213.391	
-0.172431	X_2 (p)	29.46
-0.074100	X_{21}(e)	16.68
-0.062522	X_{36}(e)	13.13
0.091039	X_{23}(e)	6.96
0.001918	X_3 (p)	8.39
0.001831	X_{37}(e)	9.65
		Total V. A.[5] = 84.28

<u>Pyrola</u> <u>secunda</u> (Y_{12})

R. C.[2]	Var.[3]	V. A.[4]
	Equation Constant = -7.12177	
0.0000129	X_{13}(e)	27.68
-0.000802	X_{12}(e)	25.84
0.0000559	X_{37}(e)	8.90
-0.002942	X_{32}(e)	7.12
5.46071	X_{30}(e)	7.71
-0.019148	X_{27}(e)	11.78
		Total V. A.[5] = 89.04

Footnotes at the end of the table on page 161

Table 29. Continued

Arnica cordifolia (Y_{13})

Equation Constant = -0.815665		
R. C.[2]	Var.[3]	V. A.[4]
0.00000027	X_{49} (v)	46.59
-0.000629	X_{37} (e)	8.55
0.017727	X_{36} (e)	7.91
-0.0000026	X_{24} (e)	6.52
0.126567	X_{9} (p)	7.74
-3.27809	X_{8} (p)	3.65
	Total V. A.[5] =	80.96

Vaccinium membranaceum (Y_{14})

Equation Constant = -45.6043		
R. C.[2]	Var.[3]	V. A.[4]
2.08569	X_{38} (e)	30.67
-12.8775	X_{8} (p)	18.25
55.3875	X_{18} (e)	7.71
0.151870	X_{9} (p)	4.42
-1.11379	X_{15} (e)	5.09
0.0000112	X_{3} (p)	3.03
	Total V. A.[5] =	69.18

[1]Prominence Value = $\sqrt{\text{frequency}}$ x absolute cover + 1
[2]Regression coefficients
[3]Environmental variable number; refer to Table 24, page 138 for names; lower case letters after variable numbers refer to "p"--physiographic, "e"--edaphic, "v"--vegetation
[4]Percentage variation of the dependent variable accounted for by each term of the equation
[5]Total percentage variation of the dependent variable accounted for by the equation

variation. The edaphic variables, (hydrogen ion concentration of the mineral soil)^3, (hydrogen ion concentration of the mineral soil)^2 and (hydrogen ion concentration of the humus layer)^2, were the next three terms in the equation and accounted for an additional 22.98% of the variation. The physiographic variables, slope angle and $\log_{10}$aspect, were the fifth and sixth terms in the equation.

Vaccinium membranaceum (Y_{14})

The equation included three edaphic variables and three physiographic variables and accounted for 69.18% of the variation of the dependent variable. The two most important terms, accounting for 48.92% of the variation, were $\log_{10}$hydrogen ion concentration of the mineral soil and $\log_{10}$aspect. The remaining independent variables of the equation were $\log_{10}$available water of the mineral soil, slope angle, available water of the mineral soil and (elevation)^3.

The equations written for the four species populations of this stratum vary markedly in their composition and arrangement of environmental variables, suggesting that each species has its own environmental dependencies. That is, each species occupies a separate niche in which it reaches its maximum development.

A somewhat surprising result of these equations

is the apparent lack of dependency of these four species populations on environment created by the tree stratum. Only the equation for *Arnica cordifolia* included a vegetation variable, $(\text{basal area})^3$, which can best be interpreted as relating to light intensity, as these two variables were strongly correlated ("r" = -0.5817). Both *Arnica* and *Vaccinium scoparium* appear to be indirectly dependent on the development of the tree stratum, as indicated by the inclusion of humus layer variables in their equations. However, in both equations these terms are of minor importance.

Pyrola secunda seems to be completely dependent on physical and chemical properties of the mineral soil. It is difficult to interpret the effect the soil texture variables, $(\text{silt} + \text{clay})^3$ and $(\text{silt} + \text{clay})^2$, may have on the population size of *Pyrola*. It is suspected, however, that these variables are representative of unmeasured environmental factors which have a more direct influence on *Pyrola*; for example, soil-water movement or soil-water conservation.

Vaccinium scoparium and *Vaccinium membranaceum*, the two most abundant herb-dwarf shrub species, appear to have quite different environmental requirements. *Vaccinium scoparium* seems to be dependent on elevation or its dependent correlates and hydrogen ion concentration of the humus and mineral soil, whereas, *Vaccinium membranaceum* appears

to be controlled by available soil-water and physiographic variables of slope angle, aspect and elevation. This difference in the environmental requirements of the two species can be used as a possible explanation for the varying population sizes of the two species in sampled subalpine stands. With such different environmental requirements, the environment could easily favour the growth and development of one while preventing the growth of the other.

In comparison with the development of the stratum as a whole, herb and dwarf shrub species seem to be less dependent on the development of the tree stratum and more dependent on physiographic variables or their dependent correlates.

Bryophyte-Lichen Stratum

Hylocomium splendens (Y_{15})

The equation included four edaphic and two physiographic variables and accounted for 76.35% of the variation of the dependent variable. The physiographic variables, $(\text{elevation})^3$ and $(\text{aspect})^3$, were the most important variables in the equation, accounting for 49.00% of the total variation. The edaphic variables all pertained to hydrogen ion concentration of the humus layer and mineral soil.

Pleurozium schreberi (Y_{16})

The equation consisted of three edaphic variables,

Table 30. Multiple Regression Equations for Two Abundant Bryophyte Species

Absolute cover is used as the dependent variable.

Hylocomium splendens (Y_{15})			*Pleurozium schreberi* (Y_{16})		
Equation Constant = 55.5373			Equation Constant = 586.065		
R. C.[1]	Var.[2]	V. A.[3]	R. C.[1]	Var.[2]	V. A.[3]
-0.0000987	X_3 (p)	35.41	0.002051	X_{17} (e)	13.61
-0.576062	X_7 (p)	13.59	1320.45	X_9 (p)	21.87
-13.3411	X_{38} (e)	5.41	-552.941	X_{46} (h)	8.19
0.949219	X_{35} (e)	8.88	-172.738	X_{50} (v)	11.77
0.000158	X_{25} (e)	6.27	18.5397	X_{26} (e)	6.63
-0.012788	X_{24} (e)	6.79	-91.1677	X_{30} (e)	6.72
	Total V. A.[4] = 76.35			Total V. A.[4] = 68.79	

[1] Regression coefficients

[2] Environmental variable number; refer to Table 24, page 138 for names; lower case letters after variable numbers refer to "p"--physiographic, "e"--edaphic, "h"--historic, "v"--vegetation

[3] Percentage variation of the dependent variable accounted for by each term of the equation

[4] Total percentage variation of the dependent variable accounted for by the equation

one physiographic variable, one vegetation variable and one historic variable; it accounted for 68.79% of the variation of the dependent variable. The most important term in the equation was (available water of the mineral soil)^3 followed by cosine slope angle. Together they accounted for 35.48% of the total variation. The third and fourth terms were $\log_{10}$practical stand age and $\log_{10}$total basal area. The remaining terms were $\log_{10}$hydrogen ion concentration of the humus layer and $\log_{10}$potassium concentration of the mineral soil.

The equations for Hylocomium and Pleurozium have only one variable in common, hydrogen ion concentration of the humus layer. Thus, it is apparent that there is very little overlap in their environmental requirements. Based on the extremely different environmental requirements of the two species, it can be hypothesized that they co-exist because competition for essential environmental factors is at a minimum.

Compared with the development of the stratum as a whole, Hylocomium has an almost identical equation, whereas, Pleurozium is less dependent on physiography and and more dependent on the development of the tree stratum and stand age.

Summary

Much of the variation in vegetation structure or

species population sizes was satisfactorily accounted for by the combination of environmental variables which appeared as terms in the regression equations. The frequent occurrence of transformed variables as terms in the equations supports the statement made on page 137; namely, that the relation between vegetation attributes and the environment is seldom linear.

Due to the mathematical "excellence" of the multiple regression equations, it would appear that they most certainly could be used to obtain rough estimates of the vegetation structure or population sizes of species in the subalpine spruce-fir ecosystem by measuring the appropriate environmental variables and solving the equations. However, accurate determinations of vegetation structure and species population sizes must necessarily wait until more environmental data are available on which to base the determinations and until the autecologies of the component species are fully understood. In gaining a knowledge of the autecologies of the major species populations of the subalpine spruce-fir forest, the equations presented in this chapter could be used to great advantage. These equations show which of the measured environmental variables are apparently most influential in controlling the development of a particular species population, and therefore, intensive study could be concentrated on these selected environmental variables and their dependent correlates.

XII ORDINATION OF STANDS

In the previous chapters, the subalpine spruce-fir ecosystem was fractionated into various parts to facilitate a description of species distributions, structural development and population structures of the major species. A partial synthesis was attempted in the preceeding chapter in which the relations between vegetation and environment were analyzed. Thus far, however, practically nothing has been said about the relations of stands to each other. Thus, this last chapter is intended to be a synthesis of the preceding ones, showing the relations between stands, based entirely on vegetational criteria.

Methods of phytosociological classification of stands can be divided into two broad groups, discrete and continuous. In general, discrete classification methods utilize distinct vegetational units and provide a hierarchical arrangement of stands. The use of distinct vegetational units tends to emphasize discontinuities of the vegetation and at the same time mask any vegetation gradients that may exist between areas.

Ordination, a continuous classification method, based on species abundance, shows relationships between stands in which spatial separation is inversely proportional to the degree of similarity between the stands. Such an

ordination technique has been developed and used by Bray and Curtis (1957) and Curtis (1959, Chapter 24); it is a versatile method of representing vegetation for which distinct units are not required. An ordination is of great value in elucidating the behaviour of individual species and showing the relation of environmental factors to the vegetation, as once the ordination has been constructed, any variable can be plotted against the framework to show its distribution. By comparison of individual species distributions on the ordination, the distinctness or otherwise of communities can be assessed (Greig-Smith 1964, page 190). Thus, this system can detect vegetational continuities as well as discontinuities.

Since the ordination procedure is flexible and allows for correlation between stands and any variables for which there are data available, it seemed to be the best system to represent the relationships between the spruce-fir stands. It was, therefore, decided to construct such an ordination.

Procedure of Construction

A method of ordination, similar to that used by Bray and Curtis (1957) and modified by Beals (1960) and La Roi (1964), was employed here. The method is based on a coefficient of similarity, which detects how much one stand has in common with another.

$$\text{Coefficient of Similarity} = \frac{2w}{a + b} \times 100$$

where the coefficient of similarity is expressed as a percentage, "a" is the sum of quantitative measures of the plants in one stand, "b" is the corresponding value for a second stand and "w" is the sum of the lesser values for only those species which are common to both stands (Oosting 1956, page 77).

The quantitative measures used in the calculations were the Prominence Values of species of the shrub and herb-dwarf shrub strata (calculation formula on page 151; list of values in Tables: 6, page 67; 8, page 70). The members of the tree stratum were not included in the calculations because stands were subjectively selected on the basis of the presence and dominance of spruce and fir and the overall physiognomy of the tree stratum.

Using computer techniques, a matrix was constructed showing the coefficients of similarity for each stand with the other 17 stands (Table 31). The coefficients were totalled for each stand and the stand having the lowest sum was considered to be the most dissimilar to all the other stands (Stand 14). Stand 14 was then used as one end of the first or X axis of the ordination. The stand showing the least similarity with Stand 14 was selected and used as the second

Table 31. Coefficient of Similarity Values for the Spruce-Fir Stands Expressed as Percentages

Stand No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1	100																	
2	55.9	100																
3	33.9	30.7	100															
4	24.8	37.7	46.4	100														
5	42.8	30.7	50.1	41.9	100													
6	56.7	35.4	47.9	39.9	67.2	100												
7	54.7	60.1	33.2	35.5	40.4	45.5	100											
8	39.3	53.5	33.5	38.2	35.7	40.8	51.8	100										
9	48.2	14.9	41.5	27.4	44.9	55.7	28.8	23.9	100									
10	40.0	24.9	58.6	35.2	45.7	46.8	38.8	44.8	43.8	100								
11	45.2	53.4	26.3	17.3	25.8	27.2	45.2	36.2	19.2	22.8	100							
12	27.6	32.4	33.4	17.3	26.0	32.2	27.6	31.8	22.4	32.3	67.5	100						
13	24.8	24.7	52.4	49.1	59.9	49.4	38.0	37.2	43.2	53.5	18.7	24.3	100					
14	19.5	43.8	28.7	31.6	23.2	25.8	28.0	48.5	14.2	35.0	17.0	19.6	35.6	100				
15	42.3	32.9	39.0	20.5	35.5	44.2	31.9	39.2	38.6	49.5	36.3	43.3	39.9	28.6	100			
16	40.9	33.8	52.6	37.7	48.2	53.0	46.3	51.9	47.4	59.9	31.0	35.0	50.1	36.9	52.4	100		
17	44.3	52.2	27.7	25.1	38.1	32.4	65.8	45.9	19.3	28.9	43.7	28.1	30.4	29.3	32.6	40.3	100	
18	31.2	38.4	30.5	20.8	43.3	33.8	33.4	38.7	22.9	33.9	41.1	40.2	26.5	33.3	52.1	45.7	49.1	100
Total	784	756	766	646	792	834	805	791	656	794	674	641	763	599	759	863	733	715

end-stand of the X axis (Stand 9). The coefficient of similarity between Stands 9 and 14 was 14.2%.

Since the ordination attempts to arrange the stands according to their dissimilarities, dissimilarity values [(Beals 1960), the distances between stands] for all stands were calculated by subtracting their coefficients of similarity from the maximum value of 85%. Eighty-five per cent was used as a maximum instead of the theoretical 100% because it was realized that a sampling error was involved, and if the same stands were resampled, identical values for species attributes would not be obtained (Bray and Curtis 1957).

The length of an axis in an ordination is equal to the dissimilarity value of the two end-stands. Therefore, the length of the X axis in this ordination was equal to $85 - 14.2 = 70.8$ units of dissimilarity. The remaining 16 stands were placed on the X axis according to their dissimilarity to the end-stands. The distance each stand was placed from the initial stand (Stand 14), along the X axis, was determined from the formula:

$$X_n = \frac{L^2 + Da^2 - Db^2}{2L}$$

where, X_n = the distance stand "n" is placed from the initial end-stand

L = the length of the X axis

Da = the dissimilarity value of stand "n" from the first end-stand

Db = the dissimilarity value of stand "n" from the second end-stand

When all the stands were located along the X axis, some very dissimilar ones were placed close together. Therefore, a second or Y axis was constructed to separate these stands. The first end-stand of the Y axis was selected as the one which was most dissimilar to both end-stands of the X axis and was situated near the centre of the X axis (Stand 11). The other end-stand was the one that was most dissimilar to, and within a distance of 7 dissimilarity units of, the first one along the X axis (Stand 4). In this way, the second axis approximates a perpendicular relationship to the first one. Stands 11 and 4 had a coefficient of similarity of 17.3%, and thus, the length of the Y axis was 85 - 17.3 = 67.7 units of dissimilarity. The other stands were located along the Y axis, as they were for the X axis. Ordination distances are given in Table 32.

To test the validity of the ordination, a simple correlation ("r") was made between inter-stand distances (spatial separation) in it and coefficients of similarity for 30 randomly-selected stand pairs. Inter-stand distances were calculated from the formula:

$$\sqrt{(X_1 - X_2)^2 + (Y_1 - Y_2)^2}$$

where two stands have the locations X_1, Y_1 and X_2, Y_2 (Bray and Curtis 1957).

The resulting correlation coefficient ("r") was -0.7891,

Table 32. Stand Locations on the Ordination

Stand No.	X Axis	Y Axis
1	56.11	21.20
2	12.69	24.65
3	44.45	48.28
4	32.16	67.68
5	51.56	46.02
6	54.06	43.45
7	36.04	27.49
8	18.45	35.25
9	70.80	41.33
10	41.05	44.16
11	37.47	0.00
12	37.89	2.22
13	40.32	56.79
14	0.00	46.88
15	42.72	20.69
16	41.76	38.81
17	26.82	19.96
18	27.04	17.65

significant at the 1% level, so indicating that the ordination yielded a close approximation of the relationship of stands to one another, based on their coefficients of similarity (Table 31, page 171). The coefficient was negative because inter-stand distances are inversely proportional to the coefficients of similarity.

Relation of Stands on the Ordination

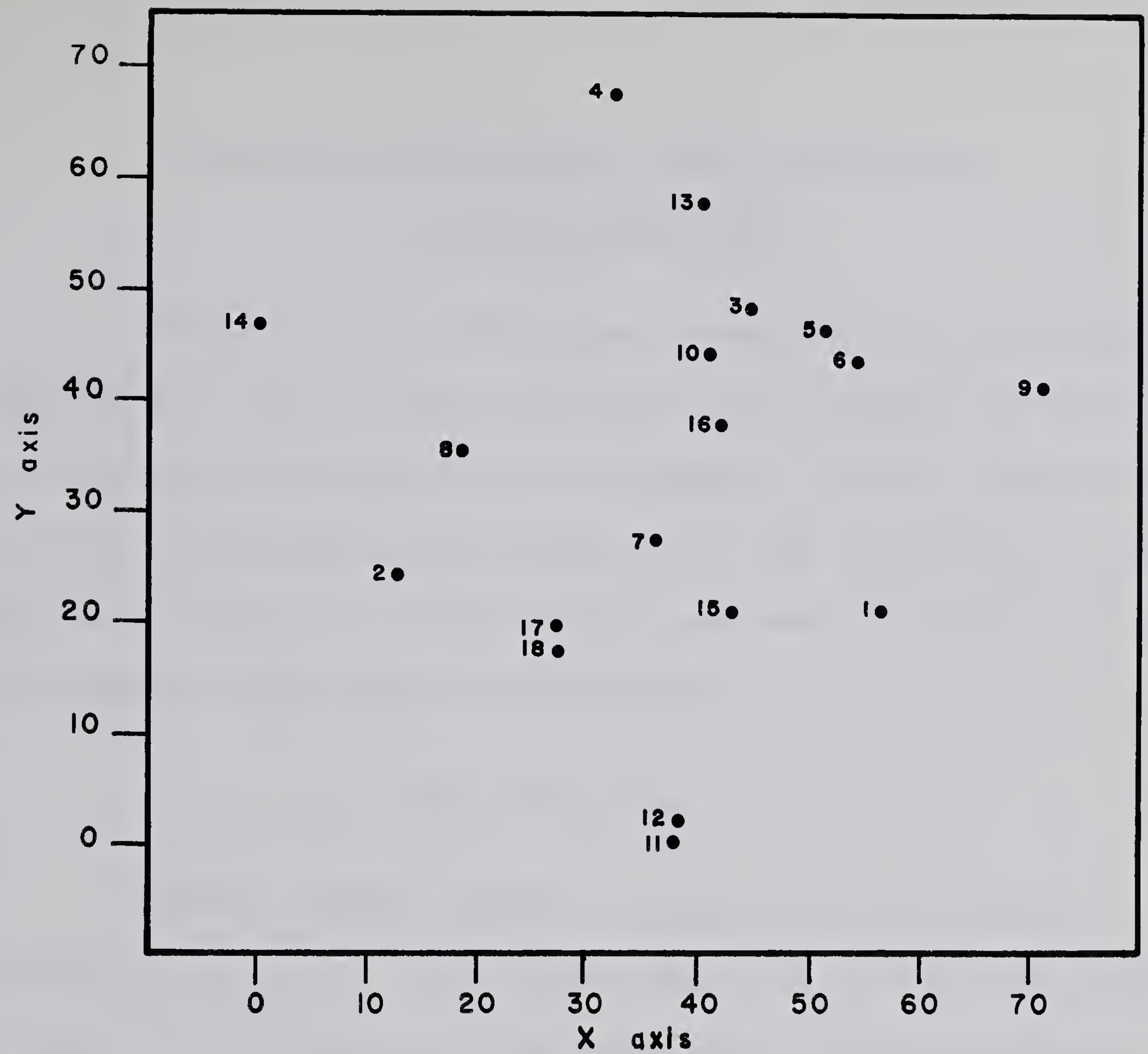
Using the values in Table 32, the locus of each stand was plotted on a two-dimensional graph by the intersection of its values on the two axes. The resulting stand ordination together with stand elevations are given in Fig. 10. The stand numbers correspond to those given on the maps in Fig.: 1, page 25; and 2, page 26.

The stands show a strong elevational orientation on the ordination, forming a parabolic curve of increasing elevation from left-to-right (Fig. 10). To a lesser extent, the stands are also arranged from left-to-right in a gradient of decreasing latitude (stand numbers are arranged in a south-to-north order). However, some stands are out of geographic context on the ordination; for example, Stands 2 and 13. Therefore, based on the spatial arrangement of stands in the ordination, it appears that the two-dimensional distributional pattern of species, outlined in Chapter VIII, is more a function of elevation than of latitude.

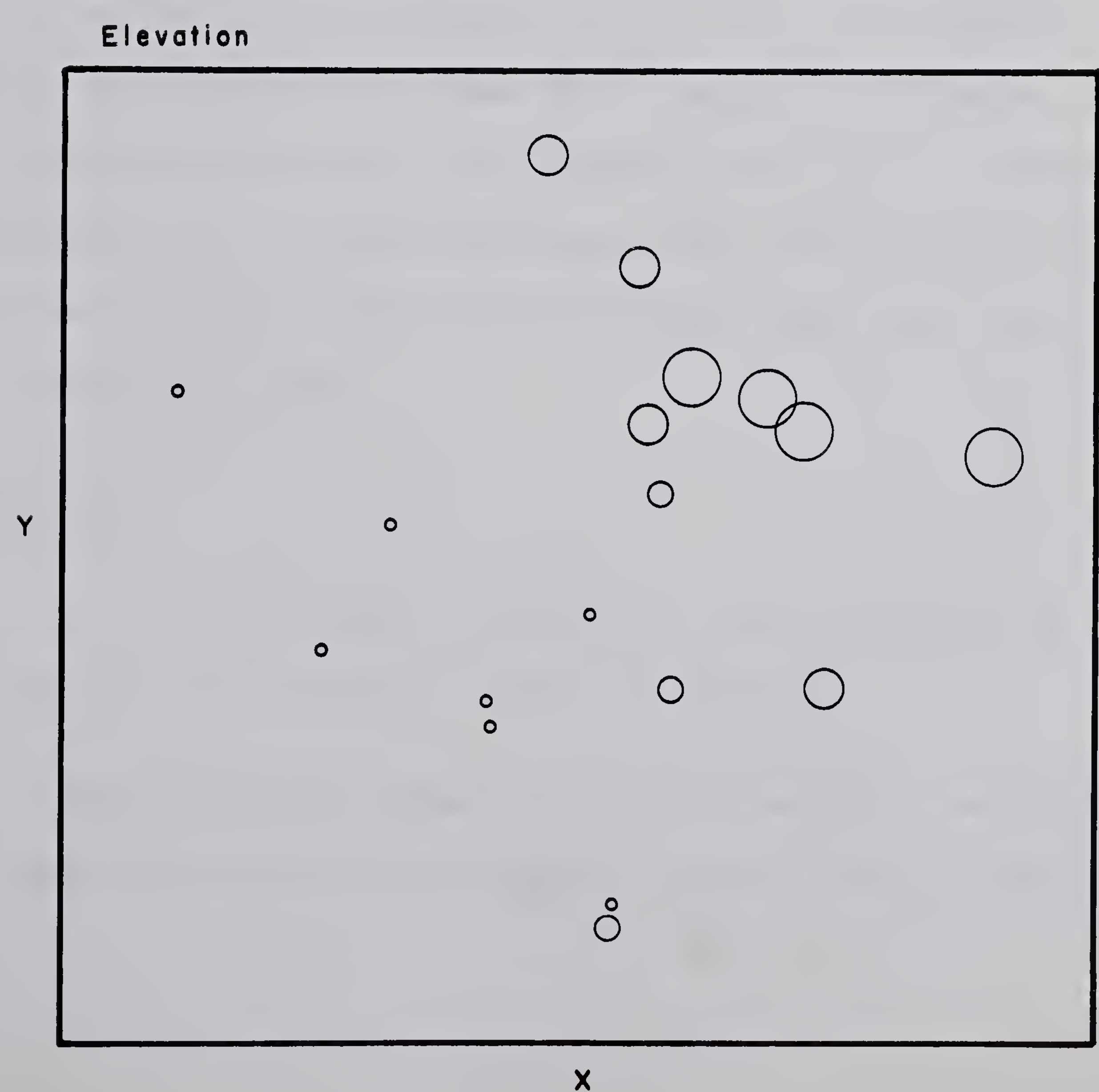
Figure 10. Location of the Spruce-Fir Stands on the Ordination and the Pattern of Stand Elevations

The stand numbers are arranged in a south-to-north order.

The four sizes of circles, from smallest to largest, represent elevations of less than 6,000 ft above mean sea level, 6,025-6,400, 6,425-6,800 and greater than 6,825.



70
60
50
40
30
20
10
0
Y axis
4
13
3
14
5
10
6
9
16
8
7
2
15
1
17
18
12
11
0
10
20
30
40
50
60
70
X axis



Elevation
Y
X

Patterns of Population Size of Species on the Ordination

Based on the ordination framework, the patterns of population size of species within the stands can be studied. The population patterns of species of the subalpine spruce-fir ecosystem are presented in the following figures, using four sizes of circles which represent different classes of the appropriate species attribute.

Tree Stratum

Spruce hybrid index, a stand characteristic, is presented in Fig. 11. The index shows an increasing gradient from left-to-right in the ordination field corresponding to the elevational gradient of Fig. 10. It appears then, that the transition from white spruce to Engelmann spruce follows closely the increasing elevational gradient; i.e., stands of low elevations have more white spruce characteristics and those of high elevations have more Engelmann spruce characteristics.

The Dominants

In Fig. 12 (page 179), basal area estimates of spruce and fir are plotted on the ordination.

The population size of spruce reaches a maximum in the upper left of the ordination, shows a sharp decline

Figure 11. Pattern of Spruce Hybrid Index Values on the Ordination

The four sizes of circles, from smallest to largest, represent index values of less than 225, 226-270, 271-315 and greater than 315.

Spruce Hybrid Index

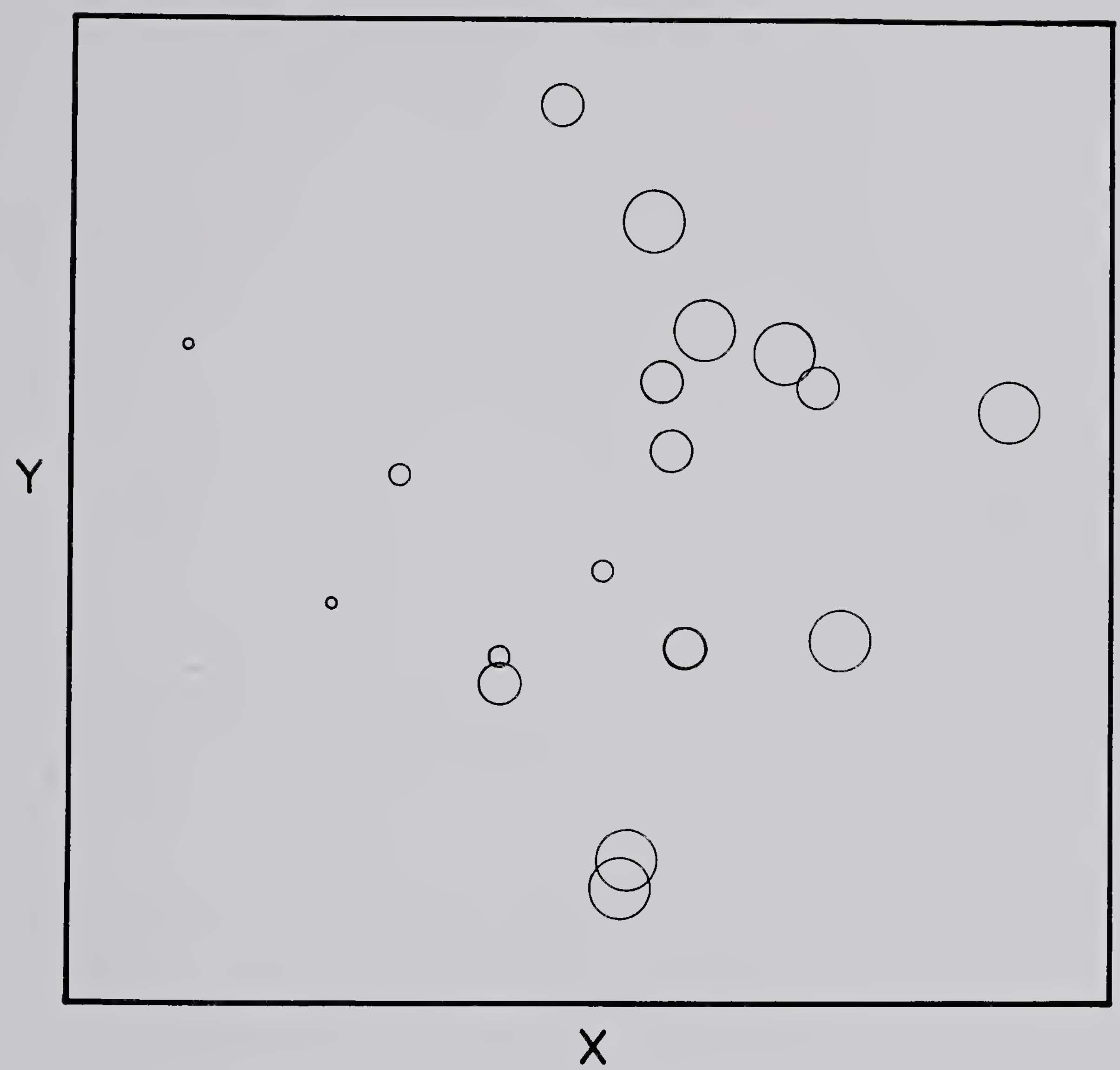
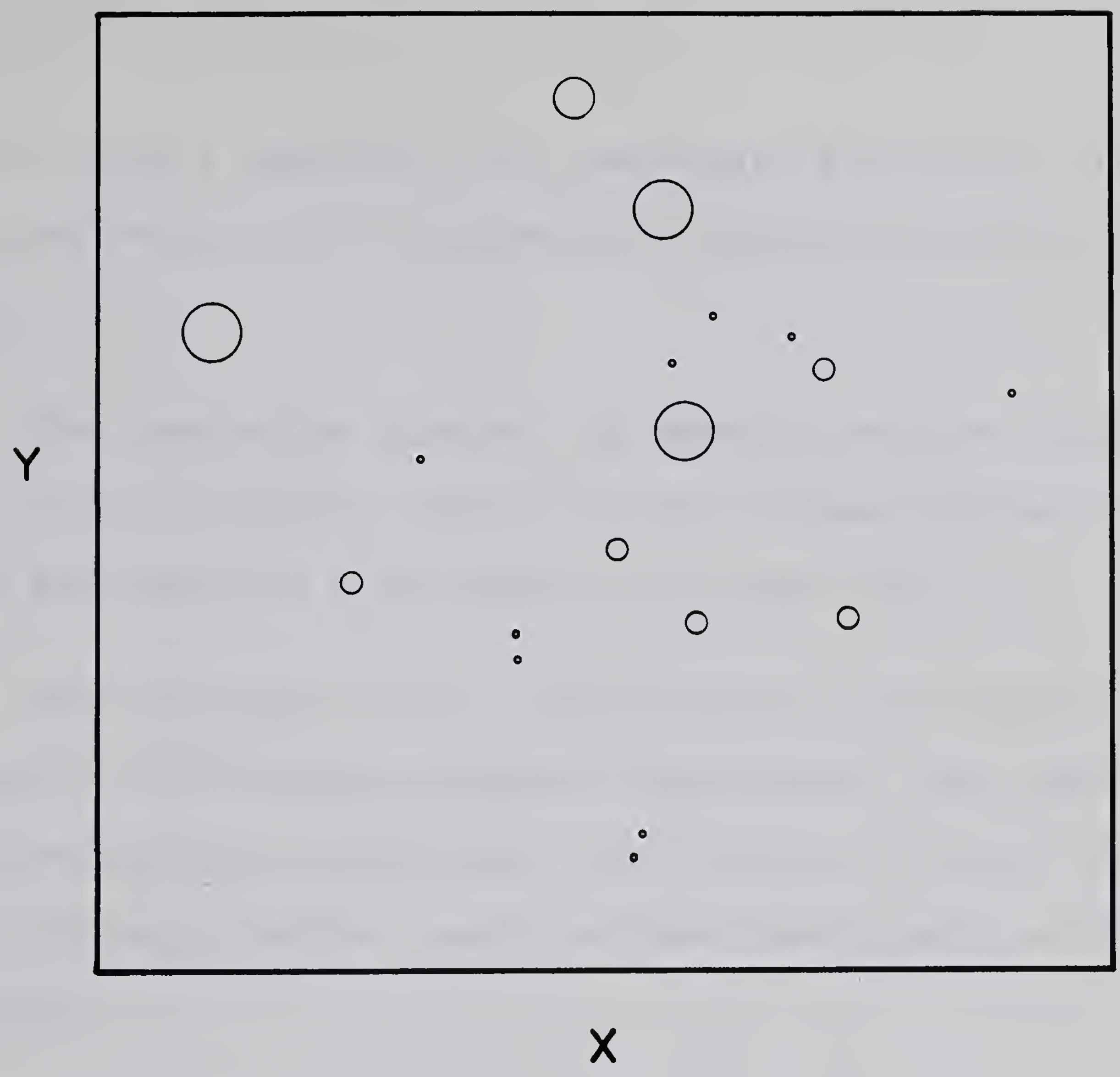


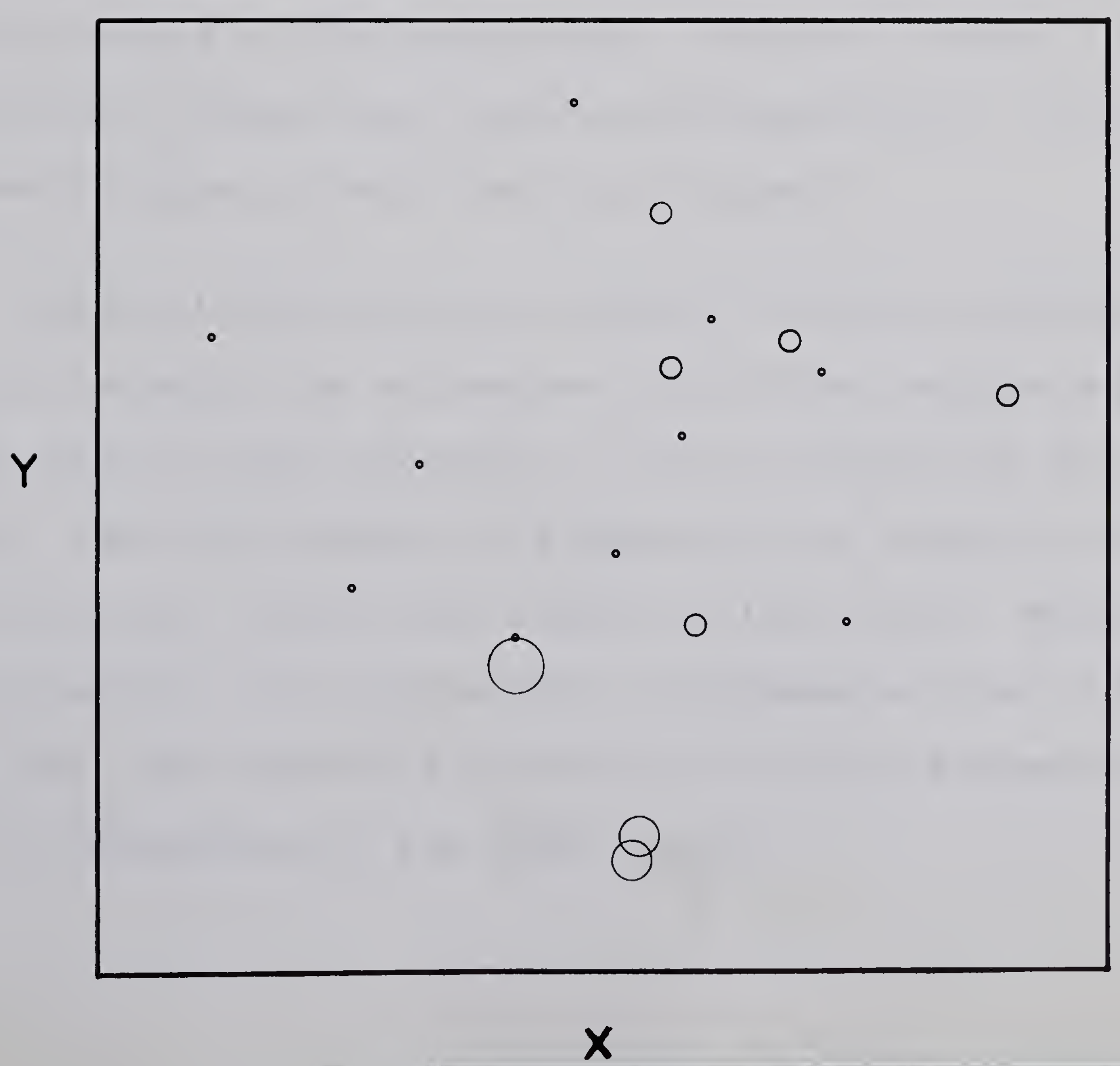
Figure 12. Patterns of Population Size of Engelmann Spruce and Subalpine Fir on the Ordination

The four sizes of circles, smallest to largest, represent basal area estimates for spruce of less than 90 sq ft per acre, 91-110, 111-130 and greater than 131; for fir, less than 60, 61-75, 76-90 and greater than 90.

ENGELMANN SPRUCE



SUBALPINE FIR



toward the central regions, has a secondary maximum in the centre, then declines to a minimum in the bottom centre of the field.

The population size of fir shows a reverse distribution to that of spruce, peaking in the bottom centre of the field and reaching a minimum in the upper left.

The behaviour of the co-dominants on the ordination supports the already-presented hypothesis, that spruce and fir show habitat preferences, and because of their different niche requirements, reach maximum development on different sites.

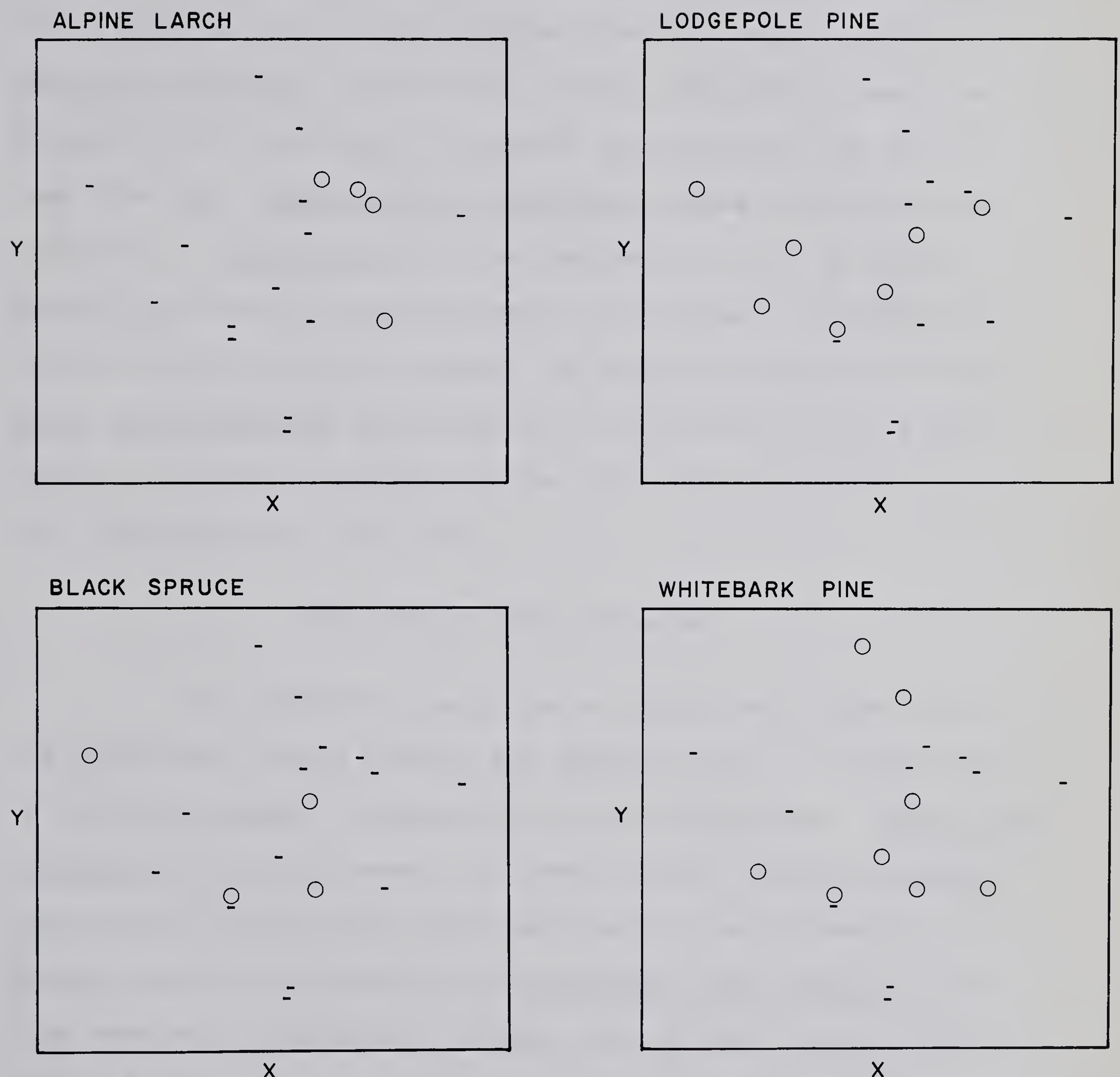
Subordinate Tree Species

In Fig. 13, presence of the four subordinate tree species is plotted on the ordination. Presence is used, as none of the four showed any significant quantitative variation between stands in which they were present.

Alpine larch occurs in stands of higher elevation on the right side of the ordination while black spruce occupies positions of lower elevation, from the centre to the left side. The distribution of lodgepole pine forms an arc from left-to-right through the centre of the field. Whitebark pine overlaps the distribution of lodgepole pine, for the most part, but extends further into the high elevation part of the ordination at the upper centre.

Figure 13. Presence Distribution of the Four Subordinate Tree Species on the Ordination

The circles indicate presence, and the dashes absence.


ALPINE LARCH
LODGEPOLE PINE
BLACK SPRUCE
WHITEBARK PINE
Y
X

Shrub Stratum

In Fig. 14, the quadrat frequencies of three major shrub species are plotted against the ordination framework. *Menziesia glabella* reaches its highest importance near the bottom of the field and is present sparingly or not at all near the top. *Rhododendron albiflorum* shows a similar distribution to *Menziesia* but its frequency is not as high. Neither species is quantitatively significant in stands in which Engelmann spruce reaches its maximum population size. *Ledum groenlandicum* approximates the distribution of black spruce, reaching a maximum on the left side and extending into the centre of the field.

Herb-Dwarf Shrub Stratum

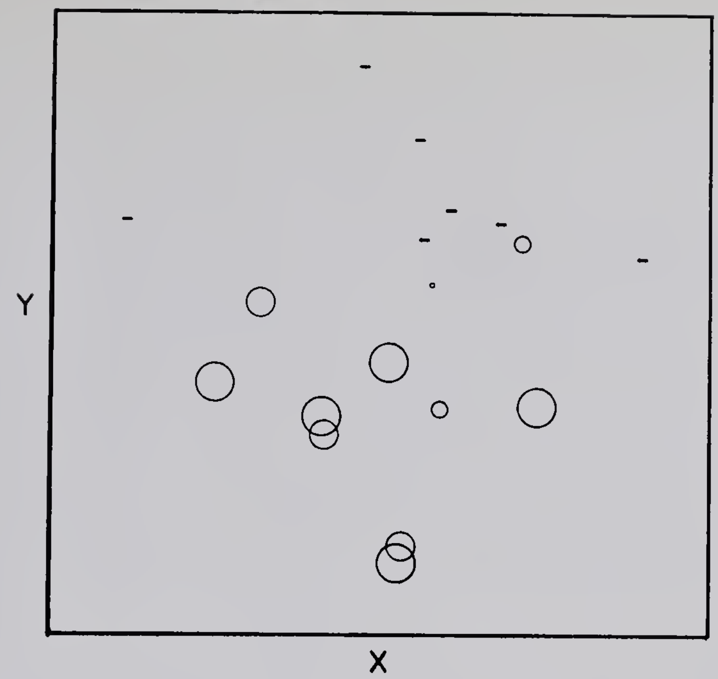
The population patterns of eight major species of the herb-dwarf shrub stratum are shown in Fig. 15 (page 184) by plotting quadrat frequencies on the ordination. *Vaccinium scoparium*, although present in every stand, reaches maximum importance in the upper right portion of the ordination. A double maximum is observed for *Vaccinium membranaceum*, with high frequency clusters on either side of the central region of the field. *Arnica cordifolia* is most abundant in the upper right and decreases through the centre toward the bottom of the field. *Elymus innovatus* shows a discontinuous distribution, being present in stands from the centre to the top of the ordination and again in stands along the

Figure 14. Patterns of Population Size of Three Major Shrub Species on the Ordination

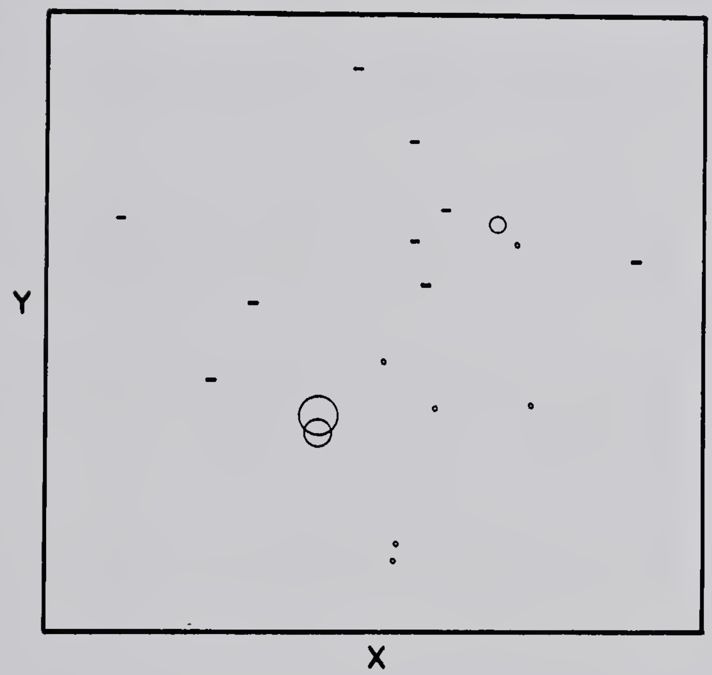
The four sizes of circles, from smallest to largest, represent quadrat frequencies of 1%-10%, 11-30, 31-60 and 61-100.

The dashes represent stands in which the species were either absent or not quantitatively significant.

Menziesia glabella



Rhododendron albiflorum



Ledum groenlandicum

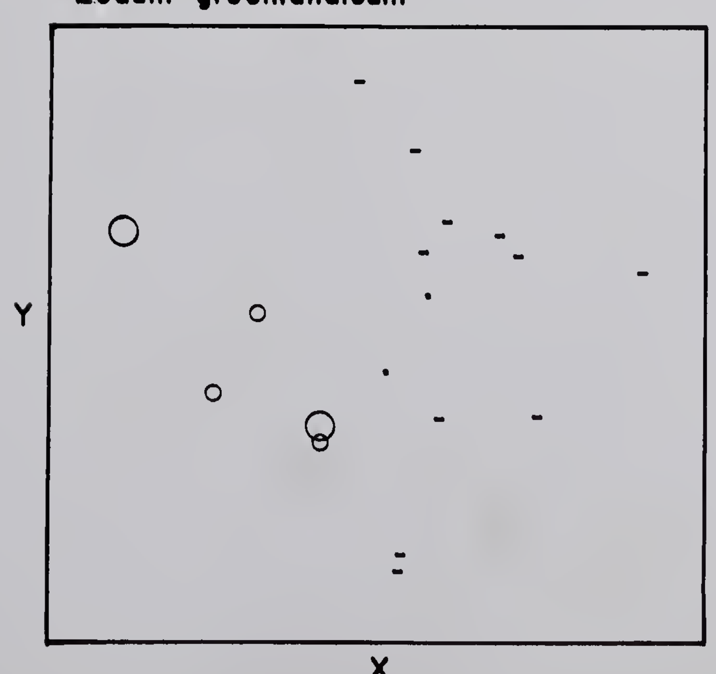


Figure 15. Patterns of Population Size of Eight Major Herb-Dwarf Shrub Species on the Ordination

The four sizes of circles, from smallest to largest, represent quadrat frequencies of 1%-10%, 11-30, 31-60 and 61-100.

The dashes represent stands in which the species were either absent or not quantitatively significant.

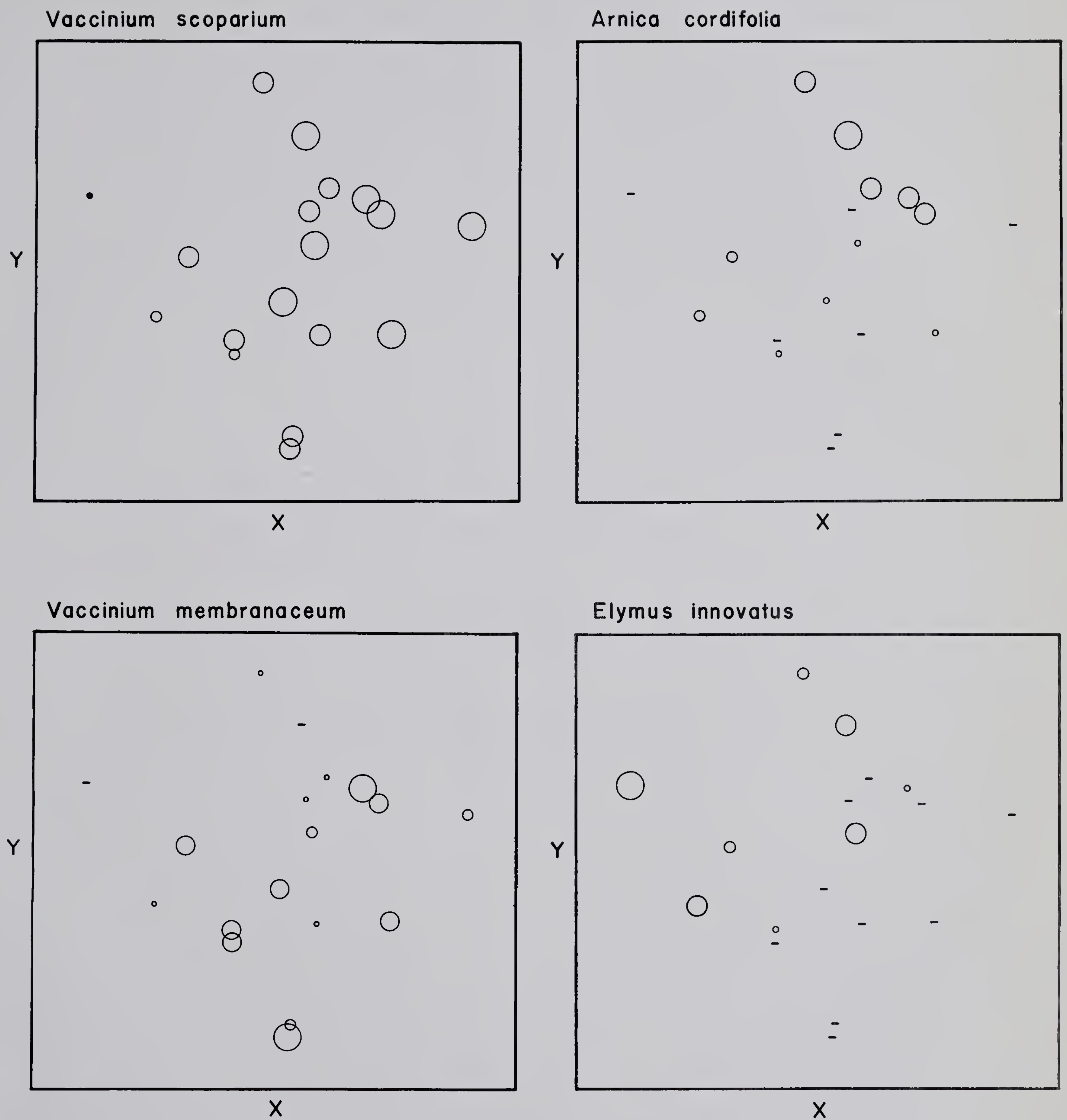

Vaccinium scoparium
Y
X
Arnica cordifolia
Y
X
Vaccinium membranaceum
Y
X
Elymus innovatus
Y
X

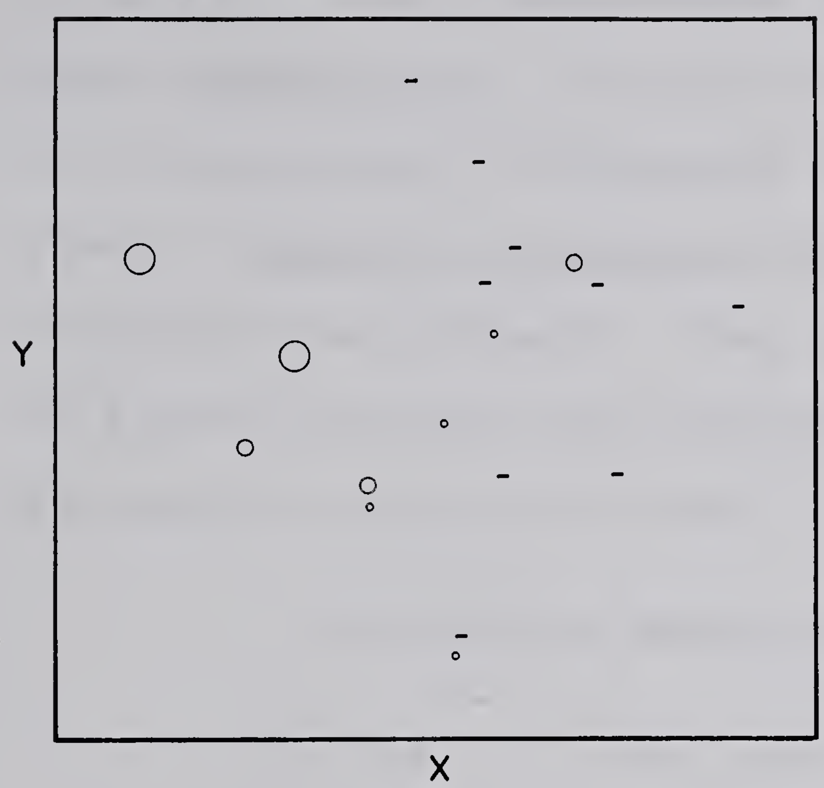
Figure 15. (Continued)

Patterns of Population Size of Eight Major Herb-
Dwarf Shrub Species on the Ordination

The four sizes of circles, from smallest to largest, represent quadrat frequencies of 1%-10%, 11-30, 31-60 and 61-100.

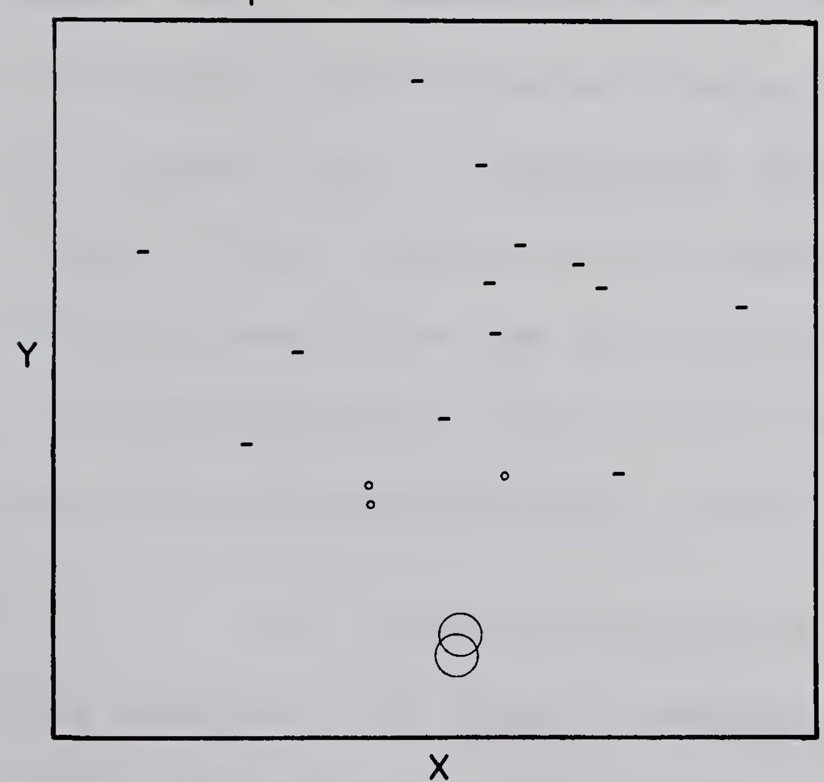
The dashes represent stands in which the species were either absent or not quantitatively significant.

Linnaea borealis



Cornus canadensis

Rubus pedatus



Lycopodium annotinum

left side. The distributions of Linnaea borealis and Cornus canadensis closely approximate those of black spruce and Ledum groenlandicum; they achieve maximum importance on the left and decrease in abundance toward the centre of the field. Lycopodium annotinum and Rubus pedatus show similar distributional patterns. They both attain population peaks at the bottom centre and decrease in abundance up through the central part of the field.

Terrestrial Bryophyte-Lichen Stratum

In Fig. 16, cover estimates of the two major bryophytes are plotted on the ordination. Hylocomium splendens shows maximum abundance at the bottom and left side of the ordination and decreases diagonally through the centre to the upper right. Pleurozium schreberi attains maximum importance at the bottom and decreases in abundance through the centre toward the top of the field. Pleurozium reaches its lowest population size in the stands which have the largest populations of Engelmann spruce.

All species represented on the ordination, with the exception of Elymus innovatus, show continuous distributional patterns. The species populations show distinct size maxima in particular parts of the field, thus, permitting visual interpretation of their ecological amplitudes.

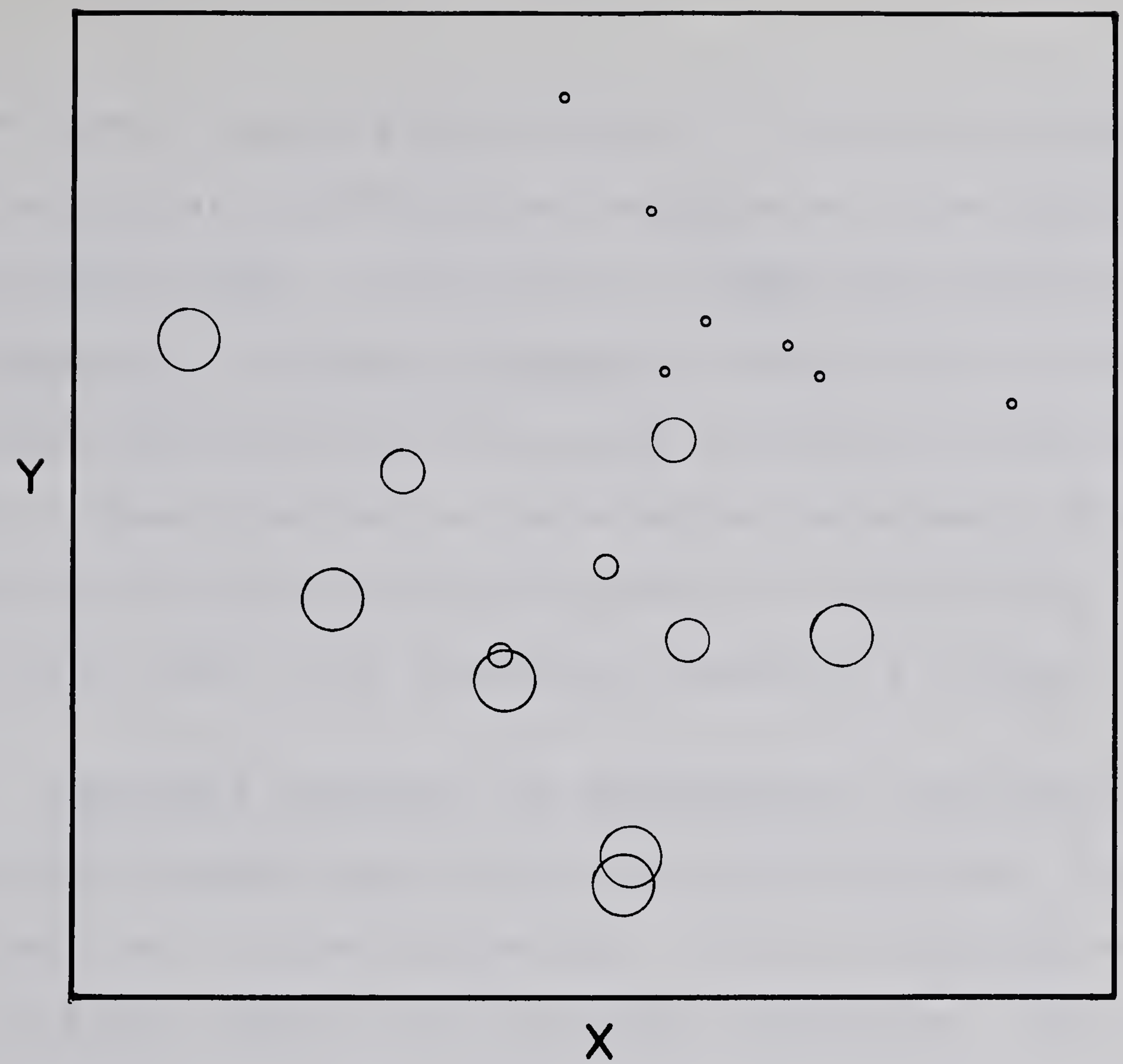
Based on the ordination, it is possible to

Figure 16. Patterns of Population Size of Two Major Terrestrial Bryophyte Species on the Ordination

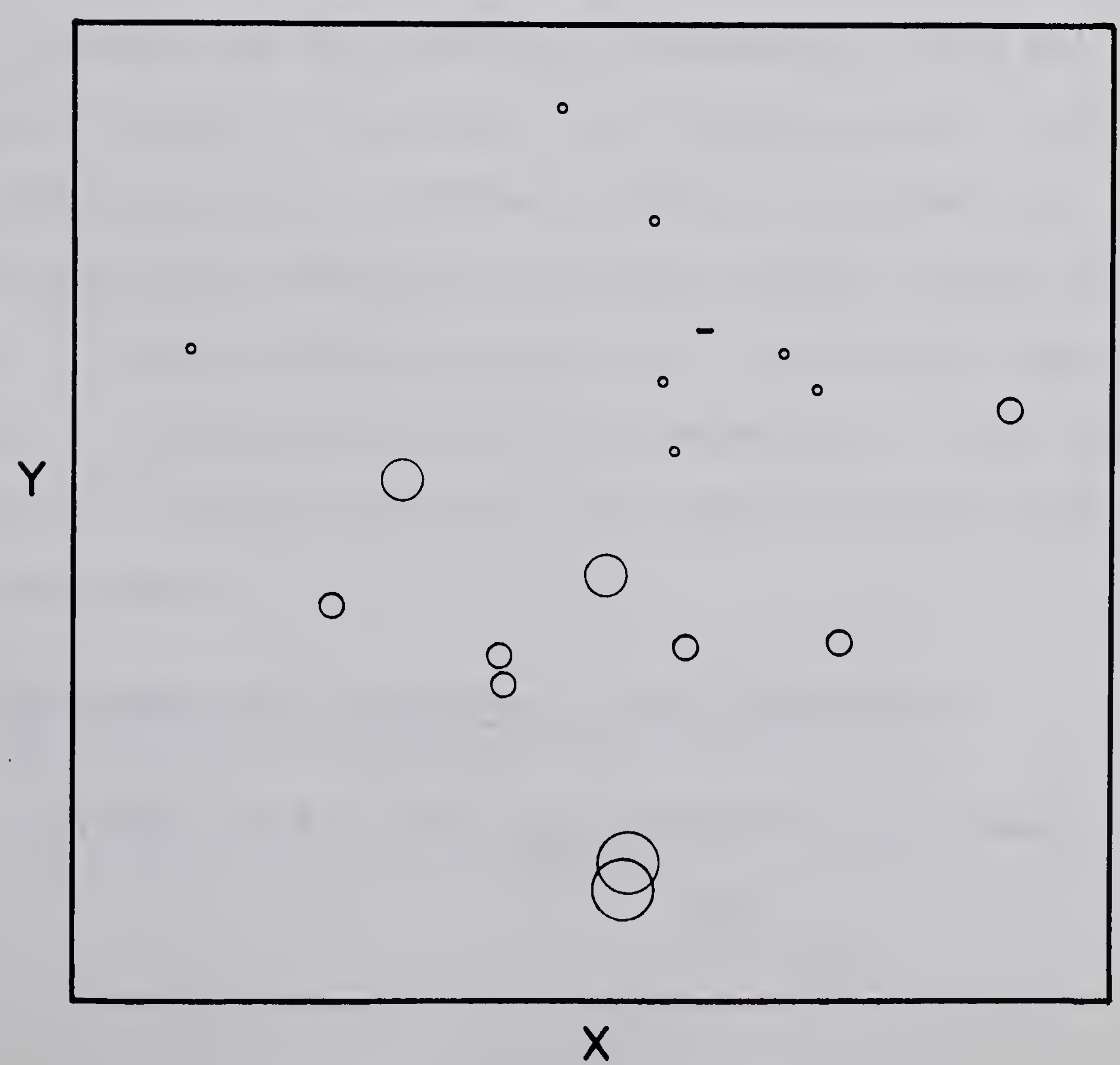
The four sizes of circles, from smallest to largest, represent cover estimates of 1%-10%, 11-20, 21-30, and greater than 31.

The dashes represent stands in which the species were either absent or not quantitatively significant.

Hylocomium splendens



Pleurozium schreberi



recognize several species associations in which the components have similar distributional patterns and overlapping ecological amplitudes. Black spruce, *Ledum groenlandicum*, *Linnaea borealis* and *Cornus canadensis* form a species association with maximum population sizes on the left side of the field. These species can be regarded as boreal influents, as they are characteristic species of much of the boreal forest where their population density is highest.

Menziesia glabella and *Rhododendron albiflorum* form a second species association with distributional maxima in the lower left of the ordination. A third association is made up of *Rubus pedatus* and *Lycopodium annotinum*. The remaining species all have individual distributional patterns and population maxima.

Because of the variety of population size patterns of subalpine spruce-fir species, and because some of the major species reach population maxima in other ecosystems, it is suggested that the subalpine spruce-fir forest cannot be documented as a clearly-defined ecosystem, but must be considered as a part of a continuously-varying vegetation. This ecosystem is related to, and not discrete from other mountain and boreal forest ecosystems.

Environmental Variables on the Ordination

In view of the results presented in the last

chapter, it is to be expected that distributional patterns of environmental factor intensities can be illustrated on the ordination framework. In addition to elevation (distribution shown in Fig. 10, page 176), the distributions of three major environmental factors are given in Fig. 17.

Stands having northeast or northwest aspects (slope exposure) are concentrated in the lower left portion of the ordination. Stands with southeast and southwest aspects occur in the upper central part of the field and those with east and west aspects are scattered across the centre.

Stands with comparatively large amounts of available phosphorus in the mineral soil are concentrated in the upper right portion of the ordination. Hydrogen ion concentration of the mineral soil forms a more complex distributional pattern. Two clusters of stands with acid soils occur at the bottom centre and upper right of the field. A belt of stands with slightly acid soils extends diagonally across the ordination, between the two acidic groups.

Summary

Based on the information presented in this chapter, it is apparent that an ordination of stands, spatially arranged by their degree of similarity, can be used to great advantage in the subalpine spruce-fir ecosystem to: (1) describe the ecological amplitudes of species, (2) show

Figure 17. Patterns of Three Influential Environmental Factors on the Ordination

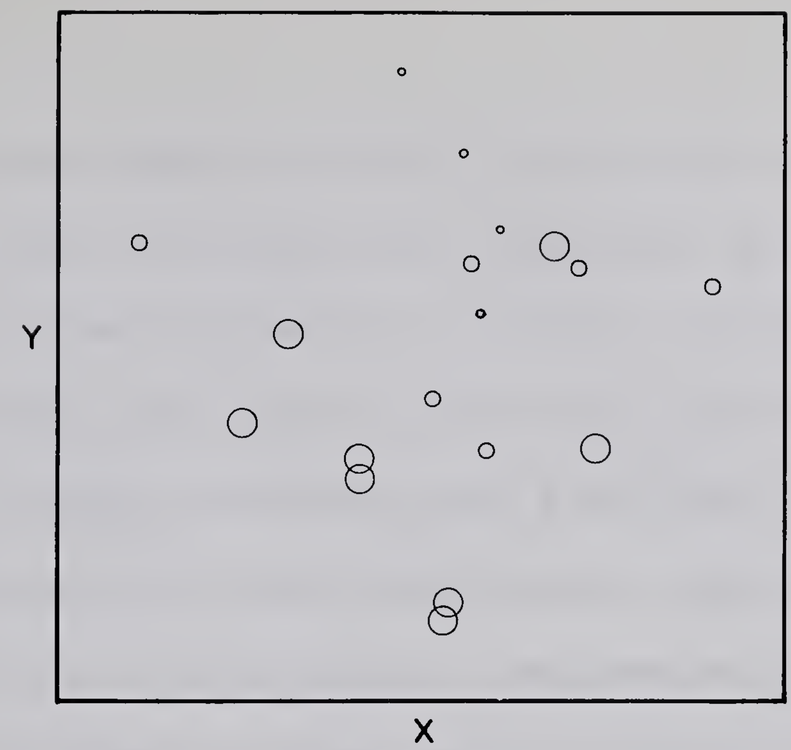
For aspect, the three sizes of circles, from smallest to largest, represent S, SE and SW, and NE and NW.

For available phosphorus concentration of the mineral soil, the four sizes of circles, from smallest to largest, represent less than 5 lb per acre, 6-10, 11-15 and greater than 16.

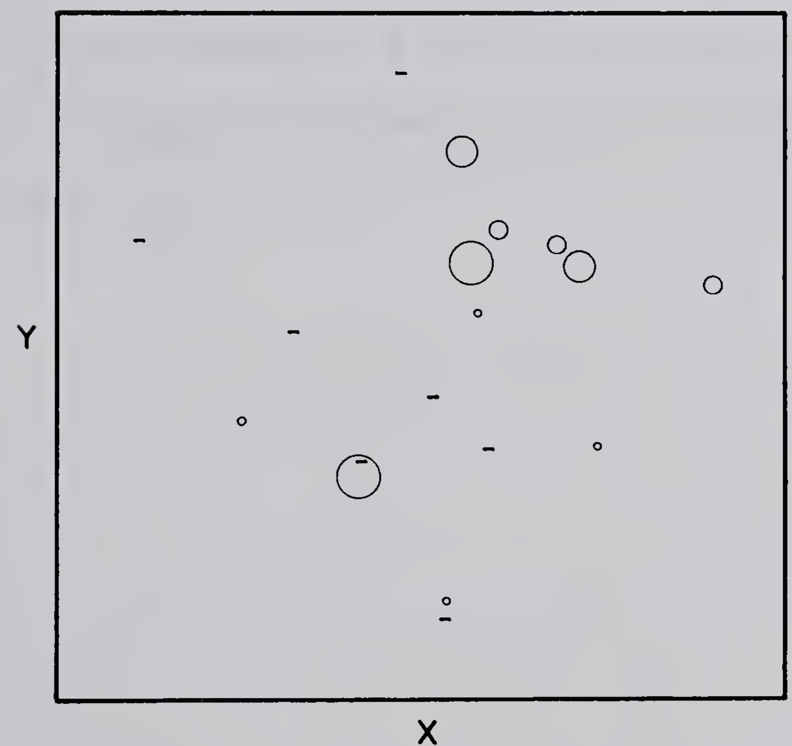
The dashes represent stands in which there was no measurable available phosphorus in the soil.

For hydrogen ion concentration of the mineral soil, the four sizes of circles, from smallest to largest, represent less than 1×10^{-6} moles per litre, 1-10, 11-20 and greater than 21.

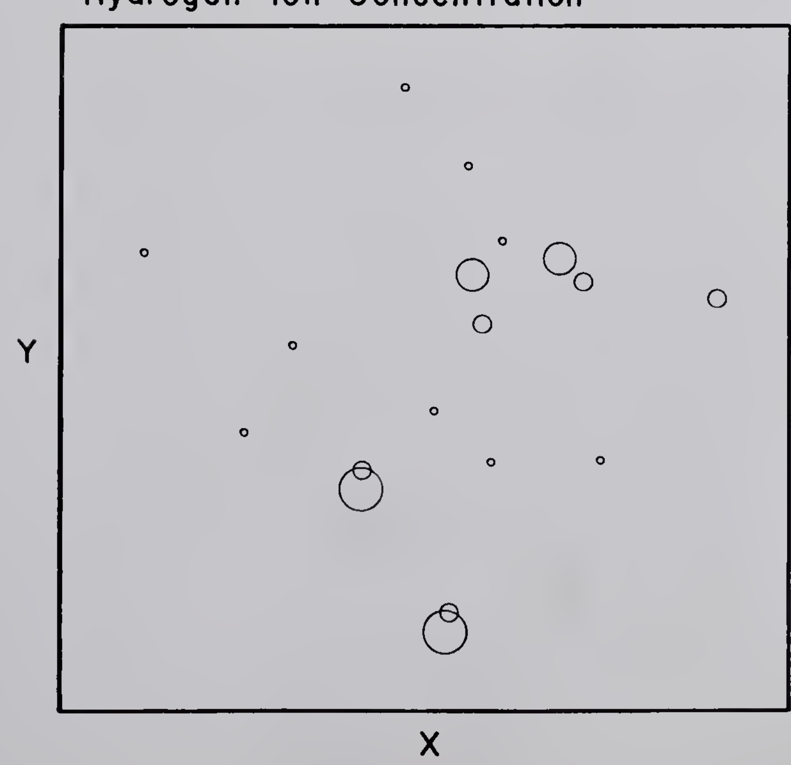
Aspect



Phosphorus Concentration



Hydrogen Ion Concentration



species associations based on their population distributional patterns and (3) give distributional patterns of the intensities of influential environmental factors. Ordination could also be used to show the relation between vegetation and environment by visually comparing the distributions of significant environmental factors and species populations. However, for an accurate evaluation of the operative environment, refined techniques such as multiple regression are necessary, as the correspondence in the distributional patterns of a vegetation parameter and an environmental factor, does not necessarily imply a direct or even indirect causal relation between the two.

XIII DISCUSSION AND CONCLUSIONS

The study upon which this thesis is based was concerned only with the Engelmann spruce-subalpine fir ecosystem, as it exists in climax condition in the subalpine zone of Banff and Jasper National Parks, Alberta. No attempt was made to describe or account for other common subalpine ecosystems: lodgepole pine forests (Horton 1956), mountain parks (Whitfield 1933), wet meadows and alpine "rain forest" (Ives 1942).

Most of the published botanical accounts of the subalpine spruce-fir forest throughout its range in the Rocky Mountains are of taxonomic, phytogeographic or forestry nature; very few ecological studies have been made. Because of this scarcity of ecological information, comparisons of the results and hypotheses of the present study with those of other workers are necessarily brief.

Oosting and Reed (1952) described the subalpine forest of the Medicine Bow Mountains, Wyoming, as a floristically homogeneous and ecologically simple association, consisting of only 46 vascular species. The results of the present study indicate that the spruce-fir forest of Banff and Jasper is floristically simple, in that 25 species populations are largely responsible for the structure of the four strata. However, the spruce-fir forest of Banff

and Jasper appears to be a good deal richer in species (total vascular flora of 113 species; Appendix C, page 220) and less homogeneous than that described for the Medicine Bow Mountains.

There appears to be a uniform structural simplicity of subalpine spruce-fir forests in the Rocky Mountains. The results of this study show only four strata to be commonly present, well-developed tree and bryophyte-lichen strata, a less well-developed herb-dwarf shrub stratum and a poorly-developed shrub stratum. A similar structural simplicity of subalpine forests was reported by Oosting and Reed (1952) in the Medicine Bow Mountains and Patten (1963) in the Madison Range, Montana.

The physiognomic characteristics of the spruce-fir forest of Banff and Jasper National Parks are its general uneven age, varying size and heights of trees together with numerous standing and fallen dead trees. These characteristics are apparently consistent in subalpine spruce-fir forests in all parts of North America, as the same physiognomy was noted by Oosting and Billings (1943) in the Sierra Nevada, Oosting and Billings (1951) in the Appalachian Mountains, Oosting and Reed (1952) in Wyoming and Langenheim (1962) in Colorado.

The spruce-fir forest of Banff and Jasper, as in other parts of the Rocky Mountains, is dominated by

relatively long-lived Engelmann spruce and relatively short-lived subalpine fir. Engelmann spruce (Picea engelmannii) is considered as a broadly-defined Linnaean species, as the results of this study and that of Horton (1959) show that stands of pure Engelmann spruce are a rarity in Alberta forests. The spruce portion of these forests is actually composed of a hybrid swarm of intermediates or genecological segregates (Heslop-Harrison 1964), between Engelmann spruce and White spruce.

In Chapter X, a description of the population structures of spruce and fir was made, patterned after the method employed by Oosting and Reed in the Medicine Bow Mountains. The results of the two studies are for the most part compatible. Spruce and fir appear to follow individual behaviour patterns throughout their life histories. Fir maintains a position in the forest by means of its prolific reproduction. However, it suffers a high mortality at all stages of development which, combined with its relatively short life-span, cause it to be less important in the forest canopy than spruce. Spruce establishes itself in low numbers but has a high survival rate which, coupled with its capacity for sustained height growth and relatively long life-span, account for it being the most important tree species. The major difference between the present study and that of Oosting and Reed is that fir was more important than spruce in some stands in Banff and Jasper.

This was suggested to be because of the different niche requirements of the two species and that, therefore, they reach population maxima on different sites, as opposed to the alternate hypothesis of a regularly occurring cycle of dominance in the climax (Rowe 1961). Oosting and Reed (1952) found no significant phytosociological differences correlated with site, exposure or altitude between stands in the Medicine Bow Mountains.

Both spruce and fir are reported to be able to reproduce asexually by layering (Cooper 1911; Cain 1941), although under closed forest conditions usually only fir layers (Horton 1959; Langenheim 1962). In the present study spruce was never found layering, but fir was observed to layer in every stand. This asexual method of reproduction was suggested as a possible explanation for the contagious population distributional pattern of fir in young stands (page 105).

Bloomberg (1950) reported that spruce-fir forests become decadent, as neither species is capable of self-perpetuation in the shade of their canopy. The results of the present study tend to refute this observation as both spruce and fir reproduction (in the form of seedlings and transgressives) was found under closed canopy conditions, with fir reproduction being more abundant than spruce. Similar findings were reported by Oosting and Reed (1952),

Reed (1952), Cormack (1953) and Horton (1959).

The two dominants are able to co-exist in a state of equilibrium because of their different life history patterns and different niche requirements. Because of the different environmental dependencies of the two species, they reach their population maxima on different sites and will remain in the same relative proportions, barring catastrophic environmental changes, with neither species succeeding the other. On the basis of the present study, it is concluded that Engelmann spruce and subalpine fir are co-dominants of a climax forest ecosystem in the subalpine zone of Banff and Jasper National Parks.

The stands used in this study were selected because they were well-defined examples of the subalpine forest as it exists in the Parks. The results indicate that it is clearly the typical Engelmann spruce-subalpine fir forest described for the Northern Rocky Mountains. Four subordinate tree species were present in the selected stands, alpine larch in southern high altitude stands; black spruce in more northerly, lower elevation stands; and whitebark pine and lodgepole pine scattered in stands throughout the study area. Based on these subordinate tree species, it is possible to place the spruce-fir forest of Banff and Jasper National Parks partly in the Northern and partly in the Far-Northern botanical provinces used by

Daubenmire (1943) in his discussion of vegetation zonation in the Rocky Mountains. Alpine larch was listed as a characteristic tree of the Northern Rockies by Rydberg (1915) and Daubenmire (1952), thus, the southern sampled stands are within the Northern phytogeographic province. Black spruce was listed by Daubenmire (1943), and Halliday and Brown (1943) as a characteristic tree of the Far-Northern Rockies, therefore, the more northerly stands fall into the Far-Northern province. However, whitebark pine was listed by several authors as a characteristic tree of the Northern Rockies (Rydberg 1915; Larsen 1930; Daubenmire 1952 and Patten 1963), and since its range overlapped that of larch and black spruce, a simple division of this forest into two botanical provinces does not seem appropriate. A more accurate placement of this forest into the zonation scheme would be partly into the Northern province (southern sampled stands), and partly into a transition zone between the Northern and Far-Northern provinces (more northerly stands), with the true Far-Northern province lying north of the study area.

The role of lodgepole pine in the sampled subalpine forest ecosystem deserves special mention. Bloomberg (1950), De Grace (1950), Cormack (1953) and Horton (1956), all working in Alberta, assigned lodgepole pine the role of a successional tree in a pyric succession. The results of the present study suggest that lodgepole

pine should not be relegated to an exclusively successional position because: (1) no stand showed signs of recent fire damage (page 78), yet lodgepole pine was present in seven stands; (2) the recorded ages of lodgepole pine were always less than the stand age; (3) lodgepole pine reproduction was found in four of the seven stands in which lodgepole pine occurred. Based on these data, it is suggested that lodgepole pine is a constant component of the subalpine spruce-fir forests of Banff and Jasper, in the role of a biological opportunist, entering and establishing itself within the forest where the climax vegetation has been locally disturbed or mechanically removed. This discussion is intended only to clarify and expand the position of lodgepole pine in the sampled subalpine forests and not to refute the fact that it is an important successional tree, as the author is in complete agreement with published reports on this point.

The results of this study show that the lower strata of the subalpine spruce-fir forest in Banff and Jasper are both structurally and floristically simple. The most important shrub species are Menziesia glabella, Rhododendron albiflorum, Ledum groenlandicum and Salix drummondiana. Of these species Cormack (1953) omitted Salix, Moss (1955) omitted only Ledum and Horton (1959) listed only Menziesia and Ledum. The shrub stratum, although poorly-developed, appears to be more prominent

than its counterpart in the Medicine Bow Mountains, described by Oosting and Reed (1952). These authors listed only one shrub species, Ribes lacaustre, and said it was of low quantitative significance.

The most abundant herb and dwarf shrub species are: Vaccinium scoparium, Vaccinium membranaceum, Lycopodium annotinum, Arnica cordifolia, Phyllodoce glanduliflora, Linnaea borealis, Elymus innovatus, Pyrola secunda, Rubus pedatus, Phyllodoce empetriformis, Cornus canadensis, Equisetum scirpoides and Cassiope mertensiana. Moneses uniflora and Pyrola virens, although not abundant, are certainly characteristic of the Banff and Jasper spruce-fir forest as indicated by their high presence values, 94% and 83% respectively. Of these species, Cormack (1953) gave the two species of Vaccinium, Lycopodium, Cornus, Equisetum, Moneses, Linnaea and Pyrola secunda; Moss (1955) omitted from his presence list the two species of Phyllodoce, Elymus and Cassiope and Horton (1959) listed only Vaccinium scoparium, Vaccinium membranaceum, Linnaea and Equisetum. Only Vaccinium scoparium, Pyrola secunda and Arnica cordifolia are in common with Oosting and Reed's presence list for the Medicine Bow Mountains.

The most abundant bryophyte and lichen species are the three feather mosses, Hylocomium splendens, Pleurozium schreberi and Ptilium crista-castrensis, along with

Dicranum scoparium, _Barbilophozia hatcheri_ and _Peltigera aphthosa_. Cormack (1953) gave _Hylocomium_, _Ptilium_ and _Peltigera_; Moss (1955) did not give a composite list of bryophytes and lichens but did mention _Peltigera_ as a common associate of the spruce-fir forest and Horton (1959) listed the three feather mosses and _Peltigera_. This well-developed bryophyte-lichen stratum, with large populations, forms the most striking difference between the spruce-fir forest of Banff and Jasper and that of the Medicine Bow Mountains, described by Oosting and Reed (1952), as these authors reported that bryophytes and lichens, although constantly present, provide negligible ground cover.

It was emphasized by Daubenmire (1943), and Oosting and Reed (1952), that while there is a high degree of floristic homogeneity in the tree stratum of the subalpine forest, there is an equally high degree of floristic heterogeneity in the dependent strata, especially with latitude. In view of this statement and the fact that several of the major species of the spruce-fir forest of Banff and Jasper are also represented in the boreal forest (page 188), two coefficients of similarity (page 170) were calculated, using presence of herb and dwarf shrub species (not quantitative data) to test the north-south and east-west similarity of the spruce-fir forest: one between the spruce-fir forest of Banff and Jasper and the Medicine Bow Mountains [data taken from Oosting and Reed (1952)], and one between

the spruce-fir of Banff and Jasper and the boreal white spruce-balsam fir [Abies balsamea (L.) Mill.] forest west of Lake Winnipeg (data supplied courtesy of Dr. G. H. La Roi). As the sampling intensity (i.e., area of sample plots expressed as a percentage of stand area) varied greatly between the three areas, only species with a presence value of greater than 20% were used in the calculations in an attempt to stabilize the results. The resulting coefficients showed a 22% similarity in floristic composition of the herb-dwarf shrub strata between Banff and Jasper and the Medicine Bow Mountains, and 40% between Banff and Jasper and the western boreal forest. Thus, it is apparent that there is almost twice as great a similarity of the herb and dwarf shrub species of the spruce-fir forest on an east-west basis than on a north-south basis, so supporting the observation that the dependent strata within the spruce-fir forest differ significantly in floristic composition at different latitudes.

In Chapter VIII, geographic and altitudinal species distributions were presented. From these distributions, it was concluded that within the subalpine spruce-fir forest of Banff and Jasper there is both a latitudinal and elevational floristic gradient. These undimensional distributions are useful in determining the range of species but give no information of varying population sizes and ecological amplitudes of the component species.

The two-dimensional ordination of stands presented

in Chapter XII, is certainly not incompatible with the single-dimension species distributions but also aids in understanding the variations in population sizes of the subalpine spruce-fir species. A second advantage of the ordination is that it can easily be extended or incorporated into a larger ordination. It is hoped that the ordination of subalpine spruce-fir stands presented in this thesis will be incorporated into the already-existing comprehensive three-dimensional ordination of the boreal forest ecosystem constructed by La Roi (1964). Such a procedure would facilitate a more accurate determination of population patterns and ecological amplitudes of the species in common to both ecosystems.

The relation between vegetation structure or species population sizes and the environment was shown with reasonably satisfactory results, using multiple regression analyses in Chapter XI. The environmental variables used in these analyses were only a very small part of the entire environmental complex, as the study was not designed, nor the researcher equipped, to measure the holocoenotic environment (Billings 1952). Data were not available for many influential environmental variables, particularly those pertaining to the summer and winter aspects (season) of climate; for example, insolation, precipitation, temperature and snow depth and duration.

Published accounts of the winter aspect of the

subalpine spruce-fir forest of Alberta are non-existent. If the entire operative environment for this ecosystem is to be synthesized, information on the winter aspect will have to be obtained. Certainly any ecosystem held under winter conditions for over eight months of the year must be profoundly influenced in its vegetational growth and development by that phase of its annual cycle.

It is hoped that the results of this study, of the subalpine spruce-fir ecosystem of Banff and Jasper National Parks in Alberta, will aid in a further understanding of the structure of the forest and the phytosociological relationships, population distributions, ecological amplitudes, and niche requirements of the component species of this widespread but little-studied subalpine ecosystem. A great deal more intensive research along the entire Cordilleran system is necessary to obtain a complete synthesis of this spruce-fir ecosystem. If such a synthesis is to be made, the time is now, while the forest still stands. To date, much of this subalpine area has survived the "axe", largely because of its inaccessibility. However, with modern technological advances in the logging industry, such protection will cease. Commercial enterprise is quickly advancing on what is one of the few remaining extensive, virgin forest ecosystems in North America. Fortunately, in Alberta much of these mountain forests are within the boundaries of National Parks, where through careful management, and a "stand-firm" policy

by interested Canadians, they will remain in their virgin condition for the "... benefit, education, and enjoyment ... of future generations" (Canada National Parks Act).

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XV APPENDICES

Appendix A

Geographic Location and Physiographic Description of the Subalpine Spruce-Fir Stands

	Geographic Location		Physiographic Description		
Stand No.	Latitude	Longitude	Elevation[1]	Aspect	Slope Angle[2]
1	51° 1.5′	115° 32′	6775 ft	NW	25°
2	51° 4.5′	115° 28.5′	5625 ft	NE	21°
3	51° 6′	115° 48′	7050 ft	SE	21°
4	51° 6.5′	115° 48′	6600 ft	SE	28°
5	51° 9′	115° 55.5′	6825 ft	NE	17°
6	51° 9′	115° 54.5′	6825 ft	W	23°
7	51° 15′	116° 2′	5950 ft	E	13°
8	51° 17.5′	115° 32′	6000 ft	NE	14°
9	51° 40′	116° 28.5′	6825 ft	E	18°
10	51° 40′	116° 27.5′	6725 ft	W	10°
11	51° 49′	116° 37.5′	6175 ft	NW	19°
12	51° 50.5′	116° 39′	5925 ft	NW	14°
13	52° 12′	117° 5′	6525 ft	SW	20°
14	52° 18.5′	117° 19′	5560 ft	W	21°
15	52° 41′	118° 2′	6300 ft	W	23°
16	52° 42′	118° 10′	6075 ft	SE	24°
17	52° 55′	117° 46′	5500 ft	NW	27°
18	53° 6.5′	117° 45.5′	5825 ft	NE	24°

[1]Feet above mean sea level; midpoint of the stand
[2]Mean value of several spot readings

Appendix B

Semi-quantitative and Qualitative Scales Used in Making Subjective Estimates

Cover-Abundance Scale

P	Very rare (only one specimen seen);	Cover infinitesmal
R	Rare (but more than one individual);	No measurable cover
+	Occasional;	Cover less than 1%
1	Common;	Cover between 1% and 5%
2	Abundant;	Cover between 5% and 15%
3	Very abundant;	Cover between 15% and 25%
4	Very abundant;	Cover between 25% and 50%
5	Very abundant;	Cover between 50% and 75%
6	Very abundant;	Cover between 75% and 100%

Vitality Scale

1 Well developed, regularly completing life cycle

2 Strong and increasing, but usually not completing life cycle

3 Feeble but spreading and/or maintaining itself, never completing life cycle

4 Occasionally germinating but not increasing beyond unsuccessful adventive

Sociability Scale

1 Growing in one place, singly; separated by wide intervals

2 Growing in small groups or clumps, often mixed with other species

Appendix B. Continued

Sociability Scale (Continued)

3 Growing in small patches or stands, these with only a few other species

4 In extensive patches or colonies, often in pure stands but not necessarily

5 In great carpets, covering large portions of ground as near pure stands

Periodicity Scale (Life Cycle Signs)

F In foliage

SF Leafless

B Buds

Fl Flowering

FR Fruiting

SD Seedling

TR Transgressive

SP Sapling

T Adult tree

Slash marks were used where more than one symbol applied to a species; for example, T/SP/TR/SD.

Appendix C

Presence List

Vascular plants organized in families as in Moss (1959); Mosses organized in families as in Bird (1964); Liverworts organized in families as in Schuster (1953); Lichens organized in families as in Bird (1966).

Vascular Plants

Equisetaceae
Equisetum arvense L.
Equisetum palustre L.
Equisetum scirpoides Michx.

Lycopodiaceae
Lycopodium alpinum L.
Lycopodium annotinum L.
Lycopodium selago L.

Pinaceae
Abies lasiocarpa (Hook.) Nutt.
Juniperus communis L.
Larix lyallii Parl.
Picea engelmannii Parry
Picea mariana (Mill.) BSP.
Pinus albicaulis Engelm.
Pinus contorta Loudon var. latifolia Engelm.

Gramineae
Calamagrostis canadensis (Michx.) Beauv.
Deschampsia atropurpurea (Wahlenb.) Scheele
Elymus glaucus Buckl.
Elymus innovatus Beal
Trisetum spicatum (L.) Richt.

Cyperaceae
Carex atrosquama Mack.
Carex concinna R. Br.
Carex concinnoides Mack.
Carex franklinii Boott
Carex raymondii Calder
Carex spp.

Juncaceae
Luzula parviflora (Ehrh.) Desv.

Appendix C. Continued

Vascular Plants (Continued)

Liliaceae
Erythronium grandiflorum Pursh
Stenanthium occidentale A. Gray
Veratrum eschscholtzii A. Gray
Zygadenus elegans Pursh

Orchidaceae
Calypso bulbosa (L.) Oakes
Goodyera oblongifolia Raf.
Goodyera repens (L.) R. Br.
Listera cordata (L.) R. Br.

Salicaceae
Salix drummondiana Barratt
Salix spp.

Betulaceae
Betula glandulosa Michx.

Polygonaceae
Oxyria digyna (L.) Hill
Polygonum viviparum L.

Portulacaceae
Claytonia lanceolata Pursh

Ranunculaceae
Aquilegia flavescens S. Wats.
Delphinium glaucum S. Wats.
Ranunculus eschscholtzii Schlecht.
Thalictrum occidentale A. Gray
Trollius albiflorus (A. Gray) Rydb.

Saxifragaceae
Leptarrhena pyrolifolia (D. Don) R. Br.
Mitella nuda L.
Mitella pentandra Hook.
Parnassia fimbriata Konig
Ribes lacustre (Pers.) Poir.
Ribes viscosissimum Pursh
Saxifraga lyallii Engler

Rosaceae
Dryas hookeriana Juz.
Fragaria virginiana Duchesne var. glauca S. Wats.
Potentilla diversifolia Lehm.
Potentilla fruticosa L.
Rosa acicularis Lindl.

Appendix C. Continued

Vascular Plants (Continued)

Rosaceae (Continued)
Rubus pedatus J. E. Smith
Sorbus sp.
Spiraea lucida Dougl.

Leguminosae
Astragalus frigidus (L.) A. Gray var. americanus (Hook.) S. Wats.
Hedysarum alpinum L. var. americanum Michx.
Hedysarum sulphurescens Rydb.

Empetraceae
Empetrum nigrum L.

Violaceae
Viola orbiculata Geyer
Viola palustris L.

Elaeagnaceae
Shepherdia canadensis (L.) Nutt.

Onagraceae
Epilobium angustifolium L.
Epilobium hornemannii Reichenb.

Umbelliferae
Osmorhiza purpurea (Coult. & Rose) Suksd.

Cornaceae
Cornus canadensis L.

Pyrolaceae
Chimaphila umbellata (L.) Bart. var. occidentalis (Rydb.) Blake
Moneses uniflora (L.) A. Gray
Pyrola asarifolia Michx.
Pyrola minor L.
Pyrola secunda L.
Pyrola virens Schweigg.

Ericaceae
Arctostaphylos rubra (Rehder & Wils.) Fern
Arctostaphylos uva-ursi (L.) Spreng.
Cassiope mertensiana (Bong.) D. Don
Cassiope tetragona (L.) D. Don ssp. saximontana (small) Porsild
Ledum glandulosum Nutt.
Ledum groenlandicum Oeder

Appendix C. Continued

Vascular Plants (Continued)

Ericaceae (Continued)
Menziesia glabella A. Gray
Phyllodoce empetriformis (Smith) D. Don
Phyllodoce glanduliflora (Hook.) Coville
Rhododendron albiflorum Hook.
Vaccinium membranaceum Dougl.
Vaccinium myrtillus L.
Vaccinium scoparium Leiberg
Vaccinium vitis-idaea L. var. minus Lodd. vaccinium sp.

Gentianaceae
Gentianella propinqua (Richards.) J. M. Gillett

Scrophulariaceae
Castilleja miniata Dougl.
Pedicularis bracteosa Benth.
Pedicularis groenlandica Retz.

Caprifoliaceae
Linnaea borealis L. var. americana (Forbes) Rehd.
Lonicera involucrata (Richards.) Banks

Valerianaceae
Valeriana sitchensis Bong.

Compositae
Achillea millefolium L.
Agoseris glauca (Pursh) Raf.
Antennaria pulcherrima (Hook.) Greene
Antennaria racemosa Hook.
Arnica cordifolia Hook.
Arnica latifolia Bong.
Arnica rydbergii Greene
Artemisia norvegica Fries
Aster conspicuus Lindl.
Aster foliaceus Lindl.
Aster spp.
Cirsium sp.
Erigeron perigrinus (Pursh) Greene ssp. callianthemus (Greene) Cronq.
Hieracium sp.
Petasites vitifolius Greene
Senecio lugens Richards.
Senecio triangularis Hook.
Senecio spp.
Solidago multiradiata Ait.

Appendix C. Continued

Mosses

<u>Ditrichaceae</u>
Ditrichum flexicaule (Schwaegr.) Hamp.

<u>Dicranaceae</u>
Dicranum fuscescens Turn.
Dicranum groenlandicum Brid.
Dicranum polysetum Sw. (D. rugosum)
Dicranum scoparium Hedw.

<u>Pottiaceae</u>
Bryoerythrophyllum recurvirostre (Hedw.) Chen
Tortella tortuosa (Hedw.) Limpr.
Tortula ruralis (Hedw.) Crom.
Tortula ruralis var. alpina Wahlemb

<u>Grimmiaceae</u>
Rhacomitrium canescens (Hedw.) Brid.

<u>Splachnaceae</u>
Splachnum ovatum (Dicks.) Hedw.

<u>Bryaceae</u>
Pohlia cruda (Hedw.) Lindb.
Pohlia nutans (Hedw.) Lindb.

<u>Mniaceae</u>
Mnium lycopodioides Schwaegr.
Mnium lycopodioides ssp. orthorrhynchum (Lindb.) Wijk & Marg.
Mnium pseudopunctatum Bruch & Schimp.

<u>Aulacomniaceae</u>
Aulacomnium palustre (Hedw.) Schwaegr.

<u>Timmiaceae</u>
Timmia austriaca Hedw.

<u>Leskeaceae</u>
Lescuraea radicosa (Mitt.) Moenk.

<u>Thuidiaceae</u>
Abietinella abietina (Hedw.) Fleisch.

<u>Amblystegiaceae</u>
Drepanocladus uncinatus (Hedw.) Warnst.

Appendix C. Continued

Mosses (Continued)

Brachytheciaceae
Brachythecium salibrosum (Web. & Mohr) B.S.G.

Entodontaceae
Pleurozium schreberi (Brid.) Mitt.

Hypnaceae
Amblystegiella jungermannioides (Brid.) Giac.
Hypnum revolutum (Mitt.) Lindb.
Ptilium crista-castrensis (Hedw.) De Not.

Hylocomiaceae
Hylocomium splendens (Hedw.) B.S.G.

Polytrichaceae
Polytrichum commune Hedw.
Polytrichum juniperinum Hedw.
Polytrichum piliferum Hedw.

Liverworts

Lophoziaceae
Barbilophozia hatcheri (Schmid.) Dumort
Barbilophozia barbata (Evs.) Steph.
Lophozia alpestris (Schleich.) Evans

Jungermanniaceae
Jamesoniella autumnalis (D. C.) Steph.

Ptilidiaceae
Ptilidium pulcherrimum (Web.) Hampe

Blepharostomaceae
Blepharostoma trichophyllum (L.) Dumort

Marchantiaceae
Marchantia polymorpha L.

Lichens

Cladoniaceae
Cladonia spp.

Appendix C. Continued

Lichens (Continued)

<u>Parmeliaceae</u>
Cetraria islandica (L.) Ach.
Cetraria nivalis (L.) Ach.

<u>Petigeraceae</u>
Nephroma arcticum (L.) Torss.
Nephroma expallidum (Nyl.) Nyl.
Peltigera aphthosa (L.) Willd.
Peltigera canina (L.) Willd. Var. rufescens (Weis.) Mudd.
Peltigera horizontalis (Huds.) Baumg.
Peltigera malacea (Ach.) Funck.
Peltigera polydactyla (Neck.) Hoffm.

<u>Stereocaulaceae</u>
Stereocaulon tomentosum Fr.

Appendix D

Soil Data

Table Dl. Soil Profile Description

Stand No.	Horizon No.	Horizon Thickness (inches)	Horizon Type[1]	Available Water Content of the Mineral Soil (%)
1	1	4	H	-
	2	3	M	18.9
	3	10	M	22.5
2	1	4	H	-
	2	2	M	29.1
	3	11	M	15.7
3	1	7	H	-
	2	10	M	14.7
4	1	4	H	-
	2	16	M	26.7
5	1	2	H	-
	2	16	M	14.7
6	1	2	H	-
	2	3	M	17.2
	3	10	M	11.7
7	1	3	H	-
	2	1	M	40.5
	3	4	M	34.8
	4	10	M	21.9
8	1	4	H	-
	2	1	M	34.8
	3	17	M	26.9
9	1	3	H	-
	2	2	M	38.0
	3	11	M	10.7

Footnotes at the end of the table on page 228

Table Dl. Continued

Stand No.	Horizon No.	Horizon Thickness (inches)	Horizon Type[1]	Available Water Content of the Mineral Soil (%)
10	1	2	H	-
	2	2	M	37.3
	3	2	M	38.7
	4	10	M	14.6
11	1	2	H	-
	2	3	M	24.0
	3	11	M	11.4
12	1	4	H	-
	2	3	M	25.0
	3	12	M	15.3
13	1	3	H	-
	2	6	M	21.2
	3	9	M	27.1
14	1	4	H	-
	2	14	M	15.7
15	1	3	H	-
	2	21	M	21.4
16	1	4	H	-
	2	20	M	21.2
17	1	5	H	-
	2	2	M	29.1
	3	1	M	20.1
	4	15	M	23.7
18	1	4	H	-
	2	2	M	26.9
	3	2	M	22.3
	4	12	M	14.7

[1]H = humus; M = mineral soil

Appendix D. Continued

Table D2. Physical Properties of the Mineral Soil

Stand No.	Horizon No.	Fraction of the Soil Less than 2 mm in Size (% by wt)	Sand Fraction[1] (% by wt)	Silt Fraction[2] (% by wt)	Clay Fraction[3] (% by wt)	Soil Type[4]
1	2	83	38.2	35.2	26.6	loam
	3	35	52.8	35.6	11.6	sandy loam
2	2	85	51.8	28.4	9.8	sandy loam
	3	37	37.8	51.6	10.6	silt loam
3	2	86	56.2	25.2	18.6	sandy loam
4	2	73	46.0	46.1	7.9	sandy loam
5	2	59	49.2	27.2	23.6	sandy clay loam
6	2	75	52.8	35.2	12.0	loam
	3	71	63.2	25.2	11.6	silt loam
	2	99	35.8	54.6	9.6	silt loam
7	3	95	38.0	54.4	7.6	silt loam
	4	88	26.2	59.6	19.2	silt loam
8	2	97	33.8	51.4	14.8	silt loam
	3	82	34.0	50.2	15.8	loam
9	2	96	31.8	53.4	14.8	silt loam
	3	72	50.0	25.0	25.0	sandy clay loam

Footnotes at the end of the table on page 231

Table D2. Continued

Stand No.	Horizon No.	Fraction of the Soil Less than 2 mm in Size (% by wt)	Sand Fraction[1] (% by wt)	Silt Fraction[2] (% by wt)	Clay Fraction[3] (% by wt)	Soil Type[4]
10	2	97	45.8	45.6	8.6	sandy loam
	3	93	46.0	48.2	5.8	loam
	4	35	58.0	26.4	15.6	loam
11	2	47	51.8	35.2	13.0	loam
	3	49	69.0	18.6	12.4	sandy loam
12	2	-	39.8	36.0	24.2	loam
	3	84	18.4	41.2	40.4	clay
13	2	91	31.2	48.6	20.2	loam
	3	93	27.8	62.6	9.6	silt loam
14	2	45	45.5	36.1	18.4	loam
15	2	83	45.2	41.4	13.4	loam
16	2	69	49.1	26.9	24.0	sandy clay loam
17	2	98	47.2	40.8	12.0	sandy loam
	3	67	82.2	13.6	4.2	loamy sand
	4	67	77.2	17.8	5.0	loamy sand

Footnotes at the end of the table on page 231

Table D2. Continued

Stand No.	Horizon No.	Fraction of the Soil Less than 2 mm in Size (% by wt)	Sand Fraction[1] (% by wt)	Silt Fraction[2] (% by wt)	Clay Fraction[3] (% by wt)	Soil Type[4]
18	2	83	43.6	40.6	15.8	loam
	3	80	48.8	38.2	13.0	loam
	4	45	54.8	31.2	14.0	sandy loam

[1] Sand = 2.00-0.05 mm
[2] Silt = 0.05-0.02 mm
[3] Clay = less than 0.02 mm
[4] Based on soil-type classification used by the Department of Soil Science, University of Alberta

Appendix D. Continued

Table D3. Chemical Properties of the Soil

Stand No.	Horizon No.	Pounds per Acre Nitrogen	Phosphorus	Potassium	(pH)
1	1	-	5	84	4.2
	2	-	6	88	5.9
	3	2	4	66	7.7
2	1	4	79	600+	5.4
	2	1	4	82	6.0
	3	3	6	82	7.6
3	1	3	17	344	5.9
	2	1	7	76	6.6
4	1	4	32	468	5.7
	2	7	-	106	7.7
5	1	4	114	600+	4.6
	2	-	7	84	4.8
6	1	3	51	600+	5.0
	2	-	23	70	4.6
	3	1	19	104	5.2
7	1	3	8	568	5.0
	2	-	18	94	4.9
	3	1	3	50	6.0
	4	1	-	32	6.1
8	1	1	1	148	4.8
	2	-	-	78	5.7
	3	3	-	82	6.9
9	1	3	93	600+	6.4
	2	-	8	130	4.5
	3	-	6	208	5.0
10	1	5	28	600+	4.7
	2	-	19	148	4.1
	3	1	-	60	5.0
	4	-	16	102	4.7
11	1	3	137	472	4.7
	2	-	-	100	4.4
	3	-	-	46	4.5

Table D3. Continued

Stand No.	Horizon No.	Pounds per Acre Nitrogen	Phosphorus	Potassium	(pH)
12	1	1	4	398	4.5
	2	-	3	116	5.2
	3	1	3	138	5.9
13	1	1	47	600+	6.0
	2	-	14	198	6.6
	3	-	3	118	7.2
14	1	2	39	600+	5.9
	2	1	-	192	7.3
15	1	1	3	166	4.9
	2	2	-	58	6.7
16	1	1	4	86	4.0
	2	-	1	50	5.2
17	1	1	4	238	4.2
	2	1	11	82	4.4
	3	9	3	82	7.2
	4	-	-	104	5.9
18	1	1	108	568	4.7
	2	-	47	152	4.2
	3	-	26	116	4.5
	4	-	19	116	4.5